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VOLUME 111 NUMBER 1

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PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA
INCLUDING
TRANSACTIONS OF MEETINGS

Volume 111

NUMBER 1



ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE, VICTORIA 3000

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PROCEEDINGS
OF THE
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ABUNDANCE, BIOMASS AND ESTIMATED PRODUCTION OF
INVERTEBRATE FAUNA ASSOCIATED WITH SEAGRASS,
HETEROZOSTERA TASMANICA, IN SWAN BAY AND AN
ADJACENT AREA OF PORT PHILLIP BAY, VICTORIA

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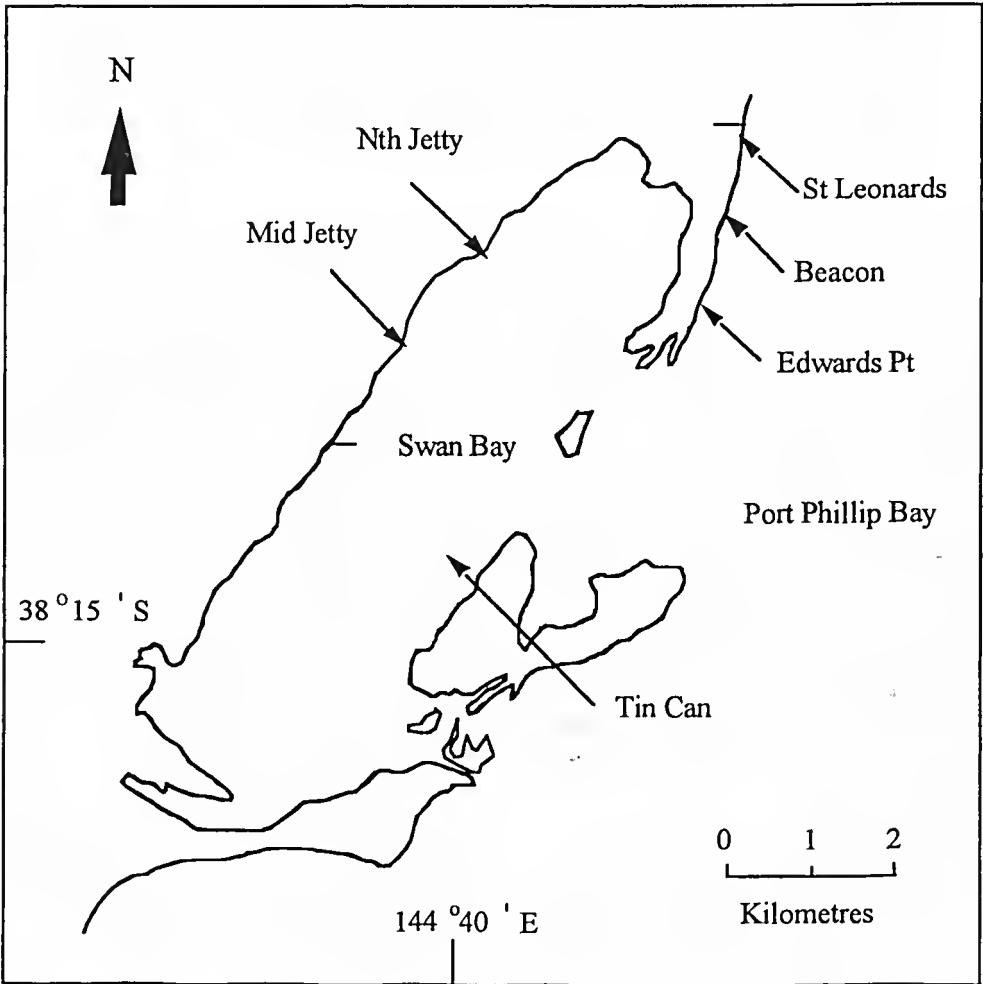
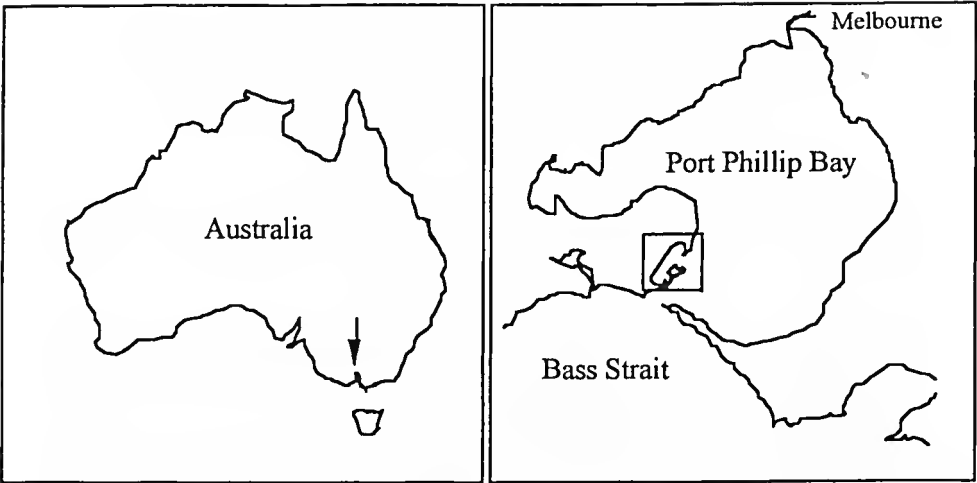
BIRD, F. L. & JENKINS, G. P., 1999:07:31. Abundance, biomass and estimated production of invertebrate fauna associated with seagrass, *Heterozostera tasmanica*, in Swan Bay and an adjacent area of Port Phillip Bay, Victoria. *Proceedings of the Royal Society of Victoria* 111(1): 1-13. ISSN 0035-9211.

Abundance, biomass and production of invertebrates were compared between Swan Bay, a seagrass system in a low energy sheltered environment, and an adjacent area of Port Phillip Bay, which had greater exposure to wave action and tidal currents. Seagrass biomass and abundances of macrofauna were not significantly different between the two areas, but organic content of sediments, biomass and production of macrofauna were significantly higher in Swan Bay. Faunal composition was markedly different, with Port Phillip Bay sites dominated by gammaridean and caprellidean amphipods, while a variety of often larger macrofaunal groups characterised Swan Bay sites. In contrast to macrofauna, the epibenthic meiofauna, dominated by harpacticoid copepods, was significantly more abundant in Swan Bay. The results support the contention that sheltered seagrass areas with elevated organic content of sediment can provide increased production of food for juvenile fish.

SEAGRASS beds are known to be highly productive environments (Hillman et al. 1989), supporting diverse and extensive communities of invertebrates. Studies comparing seagrass and unvegetated habitats have consistently found that vegetated areas sustain greater abundance and diversity of benthic invertebrates (Rainer & Fitzhardinge 1981; Poore 1982; Lewis 1984; Howard et al. 1989; Edgar 1990a) and fish (Bell & Pollard 1989; Lubbers et al. 1990; Blaber et al. 1992). Seagrass is known to trap organic debris and detritus (Norwell & Jumars 1984), with the organic material thought to enhance the secondary production (Pearson & Rosenberg 1978; Mann 1988; Spies et al. 1988). From this observation it is hypothesised that exposed habitats accumulate less detritus than sheltered habitats and would consequently have lower overall production levels. Edgar (1990a) showed by comparing a sheltered to an exposed area, that organic enrichment of sediments (by debris and detritus) enhances invertebrate production.

Swan Bay, Australia, has extensive beds of the subtidal seagrass, *Heterozostera tasmanica*, in a low energy, sheltered environment with large accumulations of debris and drift algae. The adjacent coast of Port Phillip Bay has smaller, more discrete *H. tasmanica* beds in a higher energy

environment with less accumulated debris.^{*} This area of Port Phillip Bay is adjacent to strong tidal currents associated with exchange of water through the narrow entrance at Port Phillip Heads (Black et al. 1993). Shaw & Jenkins (1992) showed that unvegetated areas of Swan Bay had finer sediments with higher organic content than unvegetated areas of the adjacent coast of Port Phillip Bay. Jenkins et al. (in review) found that fish communities in these seagrass beds were dominated by juveniles, and the abundance and biomass of fishes in Swan Bay was significantly higher than in the adjacent coast of Port Phillip Bay. Juvenile fishes at these sites consumed small invertebrates, dominated by Crustacea (Bird 1990). Edgar & Shaw (1993) found that fish and invertebrate production in Western Australia was much higher in sheltered than in exposed sites, and postulated that fishes were attracted to seagrass beds with high production of invertebrates. We postulated that the more sheltered environment of Swan Bay would result in correspondingly higher organic content of sediments and elevated production of invertebrates. In this paper, we examine this hypothesis by comparing organic content of sediments, meiofauna abundance, and macrofaunal abundance, biomass and production in Swan Bay and an adjacent area of Port Phillip Bay.



METHODS

Study area

The study area included Swan Bay and an adjacent area in Port Phillip Bay, situated on the Bellarine Peninsula, Victoria (Fig. 1). Tidal currents in Swan Bay are less than 0.05 ms^{-1} compared with currents between 0.1 and 0.5 ms^{-1} on the adjacent coast of Port Phillip Bay (Black et al. 1993). Moreover, maximum wind fetch is less than 10 km in Swan Bay, but greater than 40 km on the adjacent coast of Port Phillip Bay (Fig. 1). Two sites were sampled in Swan Bay; Tin Can and North Jetty, and two sites were sampled in Port Phillip Bay; St Leonards and Beacon. Samples were taken seasonally over two days beginning on 1 May, 1 August, 29 October 1990 and 20 January 1991. One additional site in each area, Mid Jetty and Edwards Point, was included in October for sampling of organic content of sediment and meiofauna abundance (Fig. 1).

Field methods

The invertebrate community was sampled using two sizes of corers. A 90 mm diameter PVC core, was used to take five haphazardly placed replicates, from each of the four sites on all four dates, to estimate abundance, biomass and production of macrofauna. A 32 mm diameter corer was used to obtain eight replicate samples at each of the six sites in October. Five replicates from each site were used for analysis of organic content and the remaining three for analysis of meiofauna. Both of the corers were pushed into the sediment to a depth of 10 cm to extract a constant volume of sediment. The samples were preserved in 99% ethanol mixed with Rose Bengal to make the animals more visible while sorting.

Laboratory methods

Each large-core sample was washed through a series of nested sieves of 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71 and 0.5 mm mesh. Small cores were washed through a sieve series of 0.5, 0.355, 0.25, 0.18, 0.125 and 0.063 mm mesh. Each category of invertebrate in each size class was counted. Seagrass biomass was estimated by drying the seagrass material remaining in the largest sieve

for 48 hours at 60°C . Organic content of the sediment was estimated from the small-core samples. Total contents of each sample was dried for 48 hours at 60°C and then burned in a combustion oven for two hours at 500°C . The change in weight due to the burning was recorded, and this change was considered proportional to the organic content.

Data analysis

Analysis of macrofauna was restricted to invertebrates passing through the 5.6 mm sieve because larger animals were not consumed by juvenile fish in the study area (Bird 1990), and in the case of mobile animals, would have a greater ability to avoid the corer. Core data were initially checked for homogeneity of variances using Cochran's test, and if necessary $\log(x+1)$ or square-root transformed. The data were then analysed using an analysis of variance with two bays, two sites nested within each bay, five replicates at each site, on each of four dates. Time and bay were treated as fixed factors, while sites were considered to be random factors.

The biomass of macrofaunal groups was estimated from abundance and previously determined mean weights of these groups in individual sieve-size classes (Edgar 1990b). The production of a specific size-class and type of epifaunal invertebrate was calculated using the equation developed and tested by Edgar (1990b) which relates daily macrobenthic production ($\mu\text{g/d}$) to ash-free dry weight (μg) and water temperature ($^\circ\text{C}$). The estimated production of a specific macrofaunal group in a given size class was multiplied by the number in that size class and summed for all size classes. Total daily production was estimated from the combined production values for each macrofaunal category.

RESULTS

Bay and site characteristics

Water temperatures tended to greater extremes in Swan Bay than in Port Phillip Bay (Table 1). Temperatures conform to those found by Jenkins (1986) except in October when we encountered an unseasonably warm sampling day. When

Fig. 1. Location of the sampling sites in Swan Bay and an adjacent area of Port Phillip Bay.

calculating production estimates for that date, the temperature 170°C (from Jenkins 1986) was used for all sites. No significant difference in seagrass biomass was found between bays (Table 2). The seagrass biomass values ranged from 4 to 10 g per core (628 to 1572 g.m⁻²) (Fig. 2). More detritus, seagrass debris and drift algae was observed inside Swan Bay than at the sites in Port Phillip Bay. Swan Bay sediment was shown to have a greater organic content than sediment in Port Phillip Bay (Table 3). A difference in organic content was also found between the Swan Bay sites (Fig. 3).

Sites	Date			
	May 1990	August 1990	October 1990	January 1991
North Jetty	15.5	12.1	25.0	22.3
Tin Can	14.7	10.9	25.0	21.4
St Leonards	16.4	11.5	18.9	20.2
Beacon	17.0	11.5	18.2	19.8

Table 1. Water temperature measurements taken at four sites in Swan Bay and an adjacent area of Port Phillip Bay (°C).

Source	Mean square	DF	F-ratio	P
Date	18.727	3	1.681	0.269
Bay	18.075	1	3.342	0.209
Date*Bay	9.902	3	0.889	0.499
SB sites	10.816	1	1.405	0.240
PPB sites	0.001	1	0.000	0.993
SB sites*Date	5.164	3	0.671	0.573
PPB sites*Date	17.123	3	2.225	0.094
Error	7.696	64		

Table 2. Nested analysis of variance comparing the estimated seagrass biomass in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Source	Mean square	DF	F-ratio	P
Bay	0.228	1	8.545	0.043
SB sites	0.051	2	7.385	0.005
PPB sites	0.002	2	0.306	0.741
Error	0.007	16		

Table 3. Nested analysis of variance comparing the organic content of sediments in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

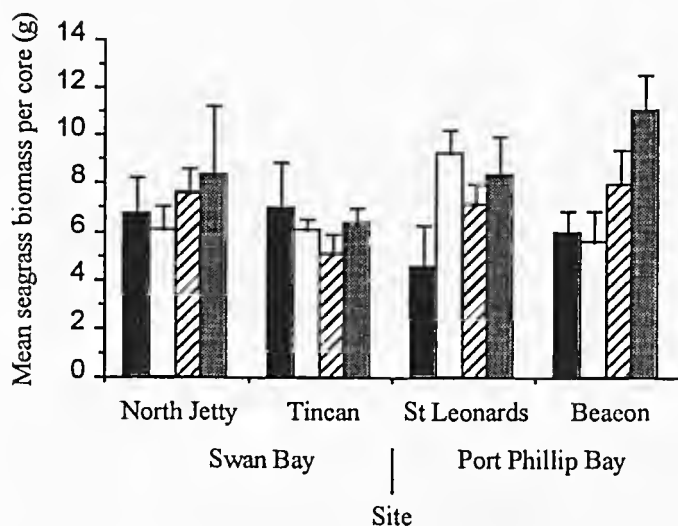


Fig. 2. Mean seagrass biomass at sites in Swan Bay and Port Phillip Bay on four sampling dates. Solid, 30 May 1990; open, 31 August 1990; diagonal, 30 October 1990; stipples, 31 January 1991. Error bars are standard error.

Macrofaunal communities

No significant difference in macrofaunal abundance was found between bays (Table 4, Fig. 4). Swan Bay had a significantly higher estimated biomass of macrofauna than Port Phillip Bay (Table 5). Macrofauna biomass also varied significantly amongst dates (Table 5). In general,

biomass of macrofauna was highest for May and August samples in Swan Bay (Fig. 4). There was also a significant interaction between abundances at sites in Swan Bay with date (Table 5). Estimated production of macrofauna for Swan Bay was also significantly higher than for

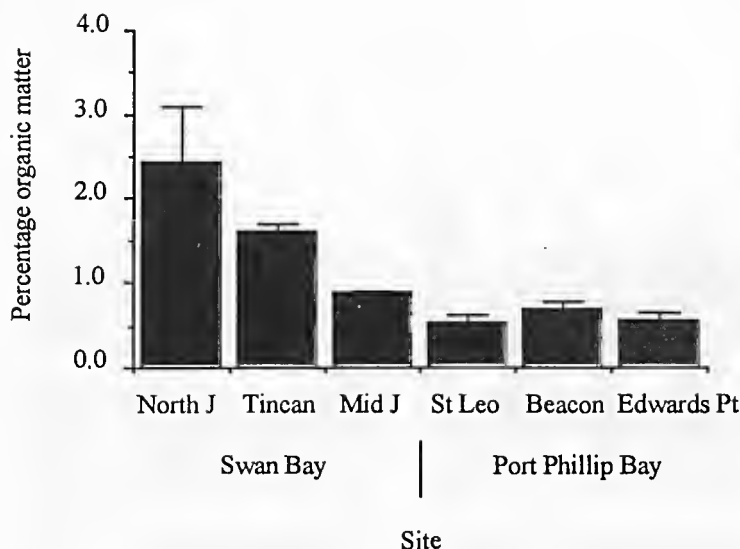


Fig. 3. Mean percentage of organic content in sediments at sites in Swan Bay and Port Phillip Bay. North J—North Jetty; Mid J—Mid Jetty; St Leo—St Leonards. Error bars are standard error.

Source	Mean square	DF	F-ratio	P
Date	19173.7	3	2.338	0.173
Bay	52173.1	1	5.600	0.142
Date*Bay	25052.4	3	3.055	0.113
SB sites	270.4	1	0.041	0.839
PPB sites	18361.2	1	2.814	0.098
SB sites*Date	14458.5	3	2.214	0.095
PPB sites*Date	1944.0	3	0.298	0.827
Error	6530.4	64		

Table 4. Nested analysis of variance comparing the abundance of macrofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Source	Mean square	DF	F-ratio	P
Date	0.046	3	1.578	0.290
Bay	2.126	1	55.900	0.017
Date*Bay	0.093	3	3.204	0.105
SB sites	0.044	1	1.972	0.165
PPB sites	0.032	1	1.435	0.235
SB sites*Date	0.048	3	2.160	0.101
PPB sites*Date	0.010	3	0.432	0.731
Error	0.022	64		

Table 6. Nested analysis of variance comparing the estimated production of macrofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Source	Mean square	DF	F-ratio	P
Date	9525.3	3	6.459	0.026
Bay	64412.6	1	104.515	0.009
Date*Bay	3381.5	3	2.293	0.178
SB sites	703.9	1	1.006	0.320
PPB sites	528.7	1	0.756	0.388
SB sites*Date	2640.9	3	3.774	0.015
PPB sites*Date	308.7	3	0.441	0.724
Error	699.7	64		

Table 5. Nested analysis of variance comparing the biomass of macrofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Port Phillip Bay (Table 6). The highest estimated production of approximately $170 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ was recorded at Tin Can in May (Fig. 4). Production estimates were also significantly different between sites in Swan Bay, however, this varied with date (Table 6). Annual production in $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at each site was estimated to be 45.5 for North Jetty, 39.7 for Tin Can, 18.6 for St Leonards and 21.2 for Beacon.

Macrofaunal communities in seagrass beds were distinctly different between the two bays (Fig. 5). Amphipods dominated in Port Phillip Bay sites; caprellid amphipods were found only in Port Phillip Bay, and gammaridean amphipods were at

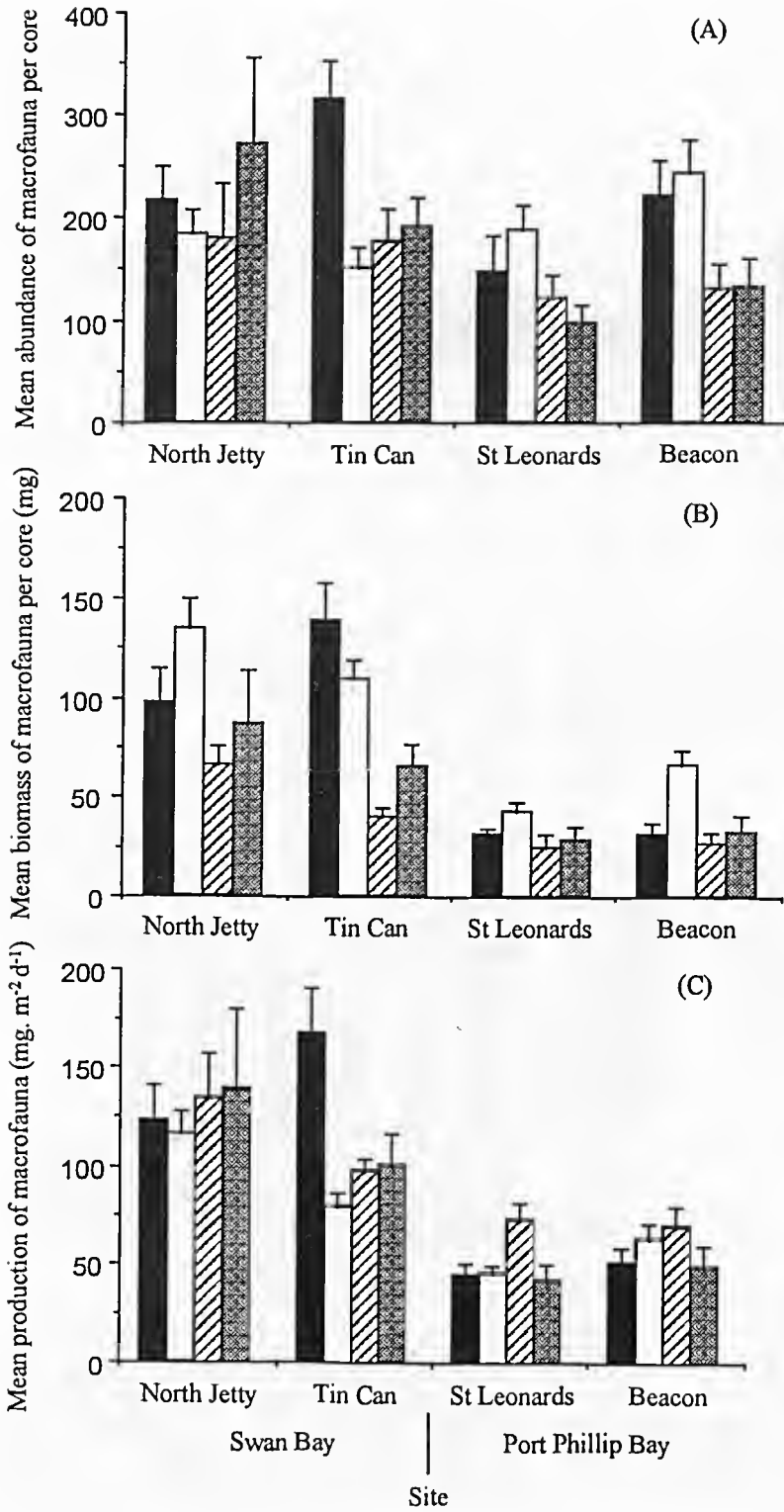


Fig. 4. Mean abundance, biomass, and estimated production of macrofauna at sites in Swan Bay and Port Phillip Bay on four sampling dates: (A) abundance; (B) biomass; (C) production. Key to dates in caption for Fig. 2. Error bars are standard error.

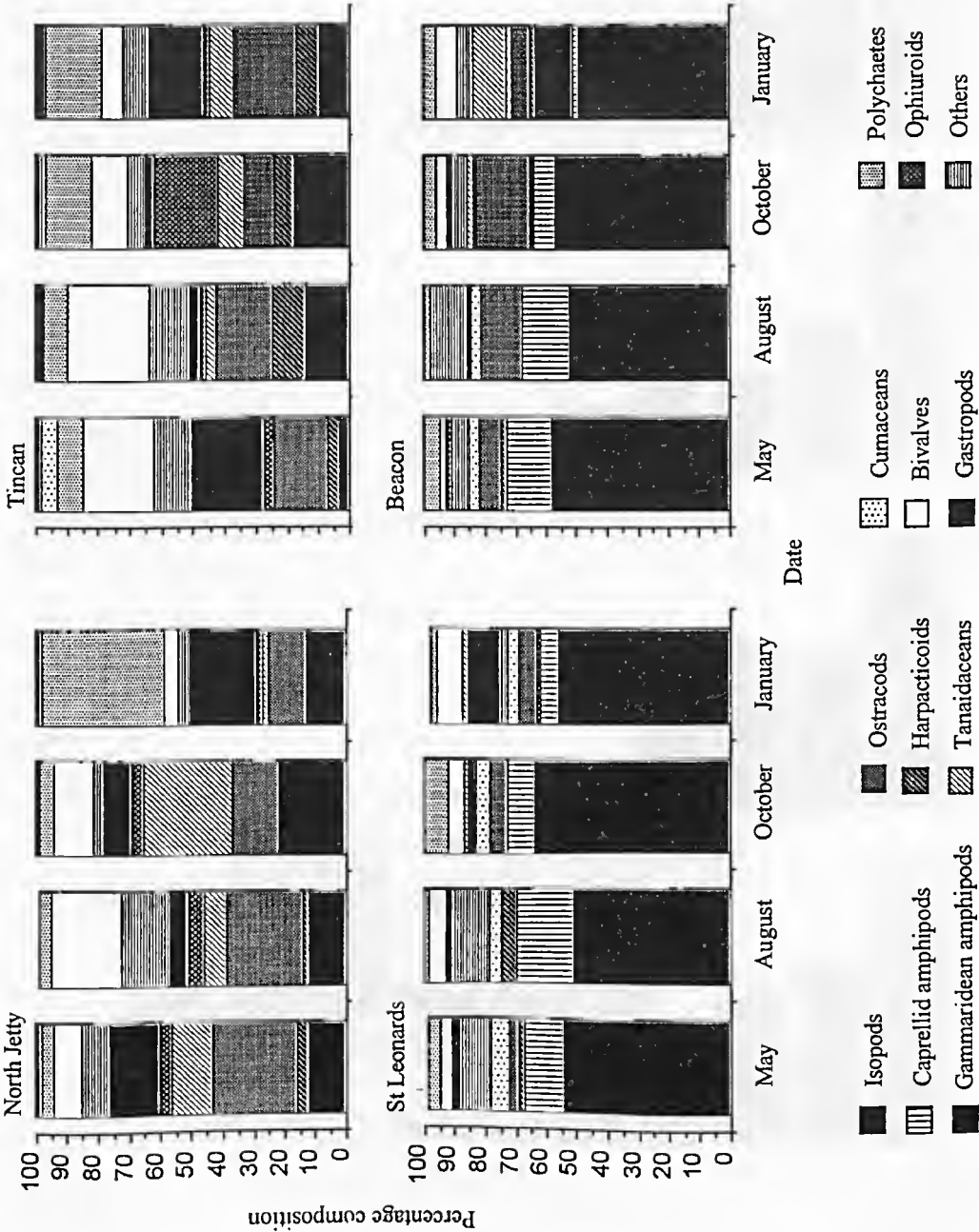


Fig. 5. Per cent composition of macrofaunal assemblages at sites in Swan Bay and Port Phillip Bay.

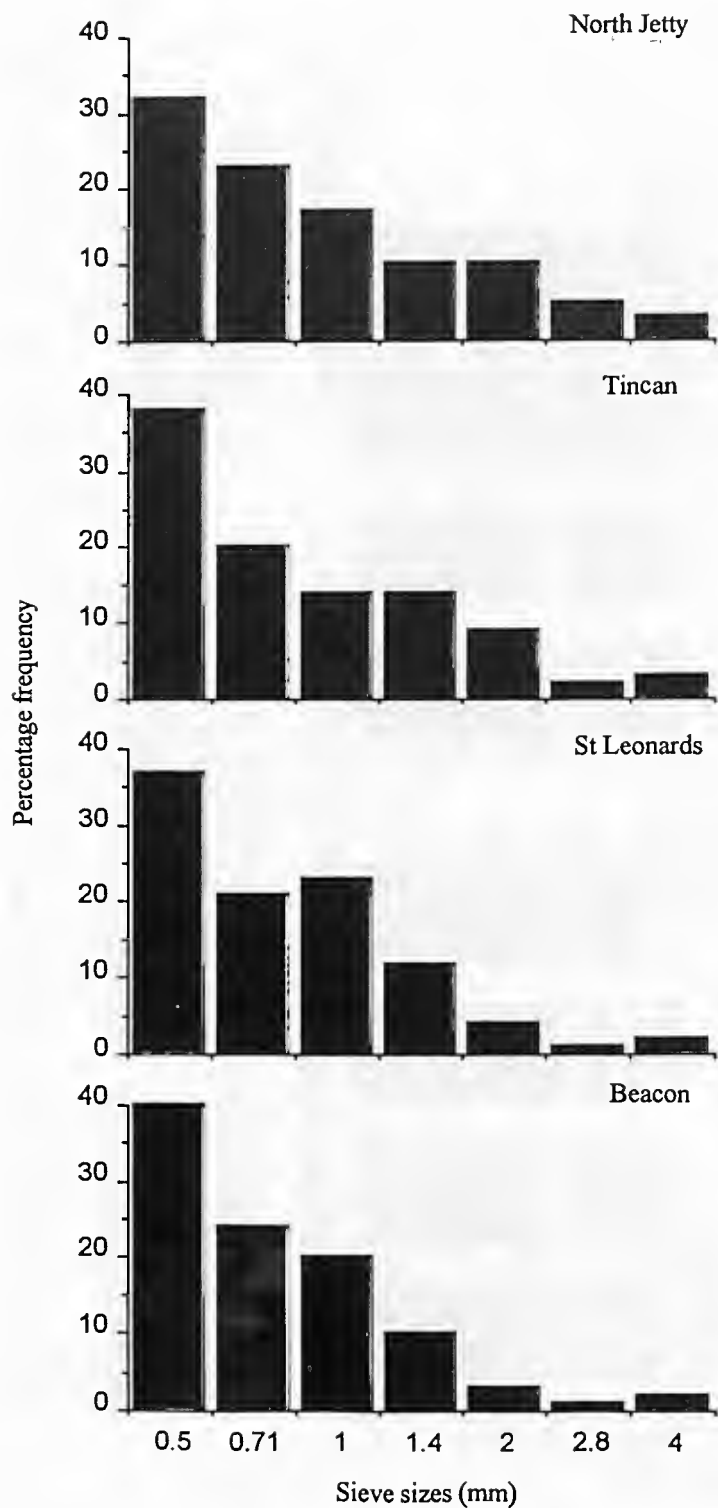


Fig. 6. Per cent frequency of macrofauna in sieve-size classes at sites in Swan Bay and Port Phillip Bay.

least three times more abundant. Cumaceans were also more abundant in Port Phillip Bay. Other invertebrates such as tanaids, gastropods and bivalves were more important at sites in Swan Bay. The January samples from Beacon were unusual in the high representation of tanaidaceans and isopods (Fig. 5). The October samples from Tin Can had unusually high numbers of ophiuroids (Fig. 5).

The size structure of the macrofaunal assemblages showed some variation amongst sites (Fig. 6). Swan Bay sites generally had a higher proportion of larger invertebrates (greater than 1.4 mm sieve size). Port Phillip Bay sites appeared to have a higher proportion of invertebrates in the 1 mm sieve-size class.

Source	Mean square	DF	F-ratio	P
Bay	101.2	1	21.463	0.010
SB sites	6.0	2	2.006	0.142
PPB sites	3.4	2	1.289	0.311
Error	2.6	16		

Table 7. Nested analysis of variance comparing the abundance of meiofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

In contrast to macrofauna, abundance of meiofauna was significantly higher in Swan Bay (Table 7). On average, meiofaunal abundance in Swan Bay was approximately four-fold that on the adjacent coast of Port Phillip Bay (Fig. 7). The major difference in the meiofaunal abundances between the two areas occurred in the 0.063 to 0.18 mm sieve-size range (Fig. 8). This was due to the presence of high abundances of epibenthic harpacticoid copepods in this size range in Swan Bay (Fig. 8).

DISCUSSION

Seagrass biomass and organic matter are two physical parameters known to be correlated with invertebrate abundance and diversity in seagrass beds. Heck & Whetstone (1977) found that invertebrate species number and abundance increased with plant biomass. Mann (1988) suggested that organic matter trapped in a seagrass bed would provide food for detritivores and Edgar (1990a) showed that organic enrichment of sediments increased invertebrate production. Edgar & Shaw (1993) found organic matter to be greater in sheltered seagrass beds than unsheltered beds, and this correlated with a higher production of invertebrates in the sheltered environments. Seagrass biomass in Swan Bay and Port Phillip Bay did not significantly differ, but the organic content of sediment was higher in Swan Bay.

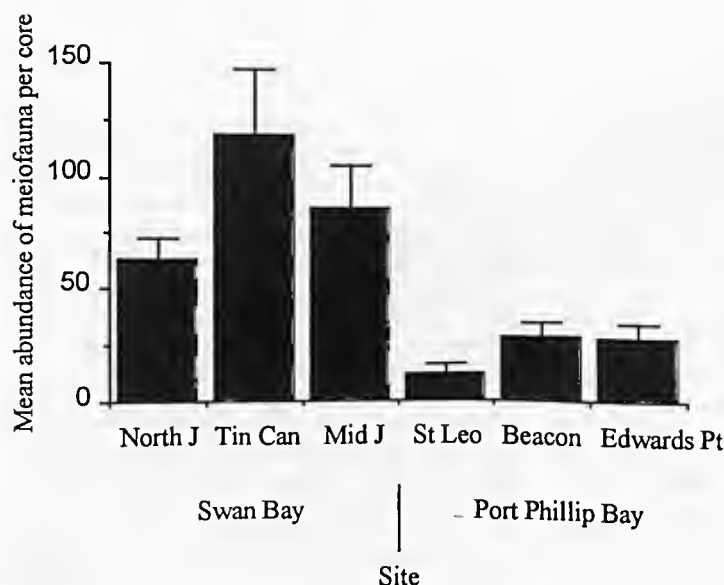


Fig. 7. Mean abundance of meiofaunal organisms at sites in Swan Bay and Port Phillip Bay on 29 October 1990. Error bars are standard error.

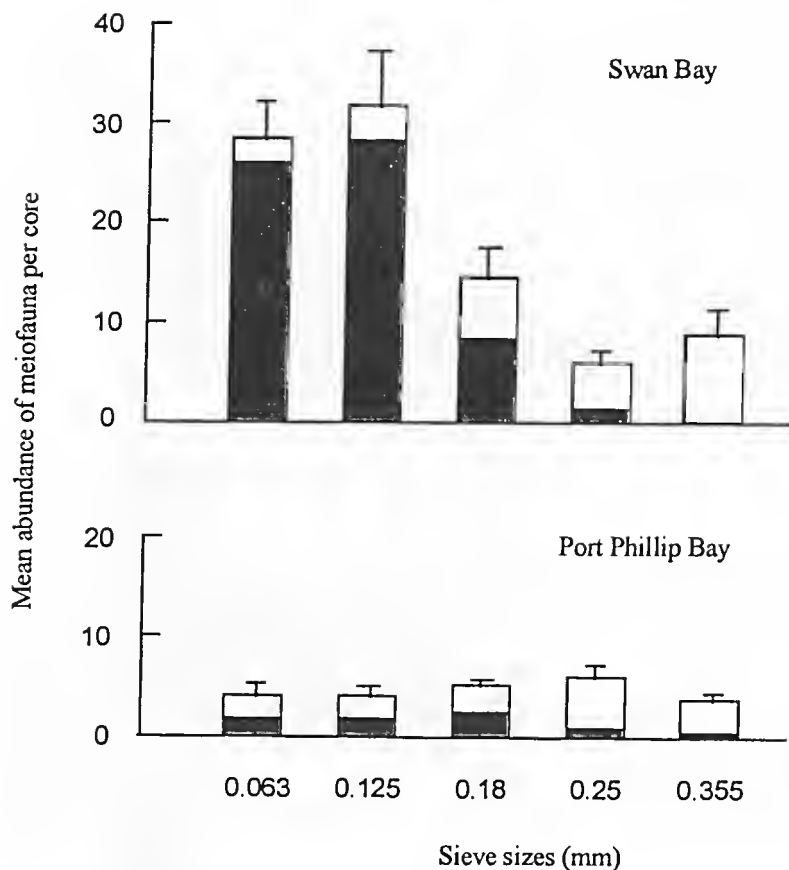


Fig. 8. Mean abundance of meiofauna of different sieve-size components in Swan Bay and Port Phillip Bay. Solid region denotes mean abundance of epibenthic harpacticoids. Error bars are standard error.

Drift algae was seen to accumulate and decompose in Swan Bay and this would enhance organic content of the sediment.

The macrofaunal communities of the two bays were distinctly different. The macrofaunal assemblages at Port Phillip Bay sites were dominated by amphipods, whereas the Swan Bay sites supported a wider range of invertebrate types. The dominance of amphipods in Port Phillip Bay may have been due to the greater exposure to wave action and currents compared with Swan Bay. Fenwick (1976) found that fauna in an algal community was influenced by wave exposure; with a high energy environment characterised by low species diversity and very high densities of amphipods. This distribution is consistent with the suggestion that animals with strong grasping appendages, such as amphipods, often dominate algal communities at exposed sites (Takeuchi et al. 1987; Hagerman 1966). The secure hold an individual has on a blade of seagrass would

protect it from the direct effect of wave and current stress.

Macrofaunal abundance gave little indication of the differences between the bays, but Swan Bay had a significantly higher biomass and estimated production of macrofauna than the adjacent area of Port Phillip Bay. This difference was probably because larger invertebrates, especially tanaids and molluscs, were more abundant inside Swan Bay than Port Phillip Bay, thus contributing more to the total biomass and production. Temperature would appear not to have been an important factor influencing production. The highest production estimates for Swan Bay were recorded in May when temperatures were lower than in Port Phillip Bay. High temperatures in Swan Bay over summer may have had a negative effect on epifaunal production by causing migration to deeper water. Differences in macrofaunal production estimated here may be underestimates if there is a difference in the available food resources in

the two areas. The equations of Edgar (1990b) were derived from a large number of field studies and would probably have included situations with varying degrees of food limitation. Food limitation in Port Phillip Bay relative to Swan Bay may be important, given the lower organic content of sediments in Port Phillip Bay, and the probable link between organic enrichment and food availability to invertebrates (Edgar 1990a).

Edgar et al. (1994) estimated epifaunal production in seagrass habitats in Westernport Bay to be $17.2 \text{ g.m}^{-2}.\text{yr}^{-1}$. This value was comparable with macrofaunal production in Port Phillip Bay which ranged between 18.6 and $21.2 \text{ g.m}^{-2}.\text{yr}^{-1}$. Swan Bay had much higher macrofaunal production levels, ranging between 39.7 and $45.5 \text{ g.m}^{-2}.\text{yr}^{-1}$. Sites sampled in Westernport Bay by Edgar et al. (1994) would have been closest to our Port Phillip Bay sites in terms of exposure to waves and currents. Our estimates would have been conservative because production estimates did not include animals larger than 5.4 mm sieve size.

Our results concur with those of Edgar & Shaw (1993), who found benthic invertebrate and fish production to be highest in sheltered environments with relatively high organic content of sediments. Organic content was probably higher in Swan Bay due to seagrass debris decaying *in situ* within beds, in contrast to the adjacent area of Port Phillip Bay where wave action would have resuspended debris which could then be transported away by tidal currents. Apart from organically enriched sediment providing increased food resources for deposit feeders (Pearson & Rosenberg 1978; Mann 1988; Spies et al. 1988), sheltered habitats with associated large surface areas of debris and stability of sediments may allow increased colonisation of periphyton food for invertebrates (Edgar & Shaw 1993).

The major difference in the invertebrate communities of the two areas occurs in the meiofaunal size range. The fact that this difference is mainly related to much higher abundances of epibenthic harpacticoid copepods is of great significance to the distribution and abundance of juvenile fish. These copepods are typically the dominant prey item of juvenile benthic fish (Feller & Kaczynski 1975; Alheit & Scheibel 1982; Hicks & Coull 1983; De Morais & Bodiou 1984; Gee 1987). Epibenthic harpacticoids were important prey items of many fish species in Swan Bay and the adjacent area of Port Phillip Bay over the period of this study (Bird 1990), and were the dominant prey of newly settled juveniles of the commercially important King George whiting in Swan Bay (Jenkins et al. 1993a). Patterns of

distribution of epibenthic harpacticoid copepods found in seagrass in the present study are very similar to those found for this group on intertidal unvegetated sediments of Swan Bay and the adjacent area of Port Phillip Bay (Shaw & Jenkins 1992). Epibenthic harpacticoids were the dominant prey of post-settlement flounder, with the result that feeding (Shaw & Jenkins 1992) and growth (Jenkins et al. 1993b) rates were significantly higher in Swan Bay.

In conclusion, the greater shelter and correspondingly higher organic enrichment of sediments in Swan Bay is associated with increased production of invertebrates, particularly in the meiofaunal size-range, compared to the more exposed coast of Port Phillip Bay. The major difference in distribution of epibenthic harpacticoid copepods, a dominant prey item for young fish, may have a significant influence on the distribution and abundance of juvenile fishes through differential habitat selection and post-settlement survival.

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REFERENCES

- ALHEIT, J. & SCHEIBEL, W., 1982. Benthic harpacticoids as a food source for fish. *Marine Biology* 70: 141-147.
- BELL, J. D. & POLLARD, D. A., 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In *Biology of Seagrasses: a Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*, A. W. D. Larkum, A. J. McComb & S. A. Shepherd, eds, Elsevier, Amsterdam. 565-609.
- BIRD, F. L., 1990. The relationship between fish predation and abundance, biomass and production of invertebrate prey in seagrass beds in Swan Bay and an adjacent area of Port Phillip Bay, Victoria. BSc(Hons) Thesis, University of Melbourne. (Unpublished.)
- BLABER, S. J. M., BREWER, D. T., SALINI, J. P., KERR, J. D. & CONACHER, C., 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. *Estuarine, Coastal and Shelf Science* 35: 605-620.

- BLACK, K. P., HATTON, D. & ROSENBERG, M., 1993. Locally and externally-driven dynamics of a large semi-enclosed bay in southern Australia. *Journal of Coastal Research* 9: 509-538.
- DE MORAIS, L. T. & BODIOU, J. Y., 1984. Predation on meiofauna by juvenile fish in a Western Mediterranean flatfish nursery ground. *Marine Biology* 82: 209-215.
- EDGAR, G. J., 1990a. The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. *Journal of Experimental Marine Biology and Ecology* 137: 215-240.
- EDGAR, G. J., 1990b. The use of the size-structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology* 137: 195-214.
- EDGAR, G. J. & SHAW, C., 1993. Inter-relationships between sediments, seagrasses, benthic invertebrates and fishes in shallow marine habitats off south-western Australia. In *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island*. F. E. Wells, D. I. Walker, H. Kirkman & R. Lettbridge, eds, Western Australian Museum, Perth, 439-442.
- EDGAR, G. J., SHAW, C., WATSON, G. F. & HAMMOND, L. S., 1994. Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Westernport, Victoria. *Journal of Experimental Marine Biology and Ecology* 176: 201-226.
- FELLER, R. J. & KACZYNSKI, V. W., 1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. *Journal of Fisheries Research Board Canada* 32: 1419-1429.
- FENWICK, G. D., 1976. The effect of wave exposure on the amphipod fauna of the alga, *Caulerpa brownii*. *Journal of Experimental Marine Biology and Ecology* 25: 1-18.
- GEE, J. M., 1987. Impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. *Marine Biology* 96: 497-510.
- HAGERMAN, L., 1966. The macro- and microfauna associated with *Fucus serratus* L., with some ecological remarks. *Ophelia* 3: 1-43.
- HECK, K. L., JNR & WHITSTONE, G. S., 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4: 135-142.
- HICKS, G. R. F. & COULL, B. C., 1983. The ecology of marine meiobenthic copepods. *Oceanography and Marine Biology Annual Review* 21: 67-175.
- HILLMAN, K., WALKER, D. I., LARKUM, A. W. D. & MCCOMB, A. J., 1989. Productivity and nutrient limitation. In *Biology of Seagrasses: a Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*, A. W. D. Larkum, A. J. McComb & S. A. Shepherd, eds, Elsevier, Amsterdam, 635-685.
- HOWARD, R. K., EDGAR, G. J. & HUTCHINGS, P. A., 1989. Faunal assemblages of seagrass beds. In *Biology of Seagrasses: a Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*, A. W. D. Larkum, A. J. McComb & S. A. Shepherd, eds, Elsevier, Amsterdam, 536-564.
- JENKINS, G. P., 1986. Composition, seasonality and distribution of Ichthyoplankton in Port Phillip Bay, Victoria. *Australian Journal of Marine and Freshwater Research* 37: 507-520.
- JENKINS, G. P., SHAW, M. & STEWART, B. D., 1993a. Spatial variation in food-limited growth of juvenile flounder, *Rhombosolea tapirina* Günther: evidence from otolith daily-increments and otolith scaling. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2558-2567.
- JENKINS, G. P., WATSON, G. F. & HAMMOND, L. S., 1993b. Patterns of utilisation of seagrass (*Heterozostera*) dominated habitats as nursery areas by commercially important fish. Victorian Institute of Marine Sciences, Technical Report 19, 100 pp.
- JENKINS, G. P., MAY, H. M. A., WHEATLEY, M. J. & HOLLOWAY, M. G., undated. Comparison of fish assemblages associated with seagrass and unvegetated habitats of Port Phillip Bay and Corner Inlet, Australia, with emphasis on commercial species. *Estuarine, Coastal and Shelf Science*. (In review.)
- LEWIS, F. G., 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. *Marine Ecology Progress Series* 19: 101-113.
- LUBBERS, L., BOYNTON, W. R. & KEMP, W. M., 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Marine Ecology Progress Series* 65: 1-14.
- MANN, K. H., 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. *Limnology and Oceanography* 33: 910-930.
- NOWELL, A. R. M. & JUMARS, P. A., 1984. Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics* 15: 303-328.
- PEARSON, T. H. & ROSENBERG, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review* 16: 229-311.
- POORE, G. C. B., 1982. Benthic communities of the Gippsland Lakes, Victoria. *Australian Journal of Marine and Freshwater Research* 33: 901-915.
- RAINER, S. F. & FITZJARDINGE, R., 1981. Benthic communities in an estuary with periodic de-oxygenation. *Australian Journal of Marine and Freshwater Research* 32: 227-243.
- SHAW, M. & JENKINS, G. P., 1992. Spatial variation in feeding, prey distribution and food limitation of juvenile flounder *Rhombosolea tapirina* Günther. *Journal of Experimental Marine Biology and Ecology* 165: 1-21.

- SPIES, R. B., HARDIN, D. D. & TOAL, J. P., 1988. Organic enrichment or toxicity? A comparison of the effects of kelp and crude oil in sediments on the colonization and growth of benthic infauna. *Journal of Experimental Marine Biology and Ecology* 124: 261-282.
- TAKEUCHI, I., KUWABARA, R., HIRANO, R. & YAMAKAWA, H., 1987. Species compositions of the Caprellidea (Crustacea: Amphipoda) of the Sargassum zone on the Pacific coast of Japan. *Bulletin of Marine Science* 41: 253-267.

REVISION OF *PRELISSORHYNCHIA* XU & GRANT, 1994 (BRACHIOPODA)
FROM THE UPPER PERMIAN OF SOUTH CHINA

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CHEN, Z. Q. & SHI, G. R., 1999:07:31. Revision of *Prelissorhynchia* Xu & Grant, 1994 (Brachiopoda) from the Upper Permian of South China. *Proceedings of the Royal Society of Victoria* 111(1): 15–26. ISSN 0035-9211.

A revision of the genus *Prelissorhynchia* Xu & Grant, 1994 is carried out based on an examination of the type material of '*Pugnax*' *pseudoutah* Huang (1933) from the Late Permian of South China. The systematic study of the South Chinese specimens shows that specimens previously assigned to Huang's species should be divided into two genera: *Prelissorhynchia* Xu & Grant (1994) and *Neowellerella* Dagys (1974). As a result of this revision, *Prelissorhynchia pseudoutah* (Huang) is interpreted to have a more restricted stratigraphical and geographical distribution than previously thought.

SINCE Huang (1933) proposed *Pugnax pseudoutah* for several Changhsingian specimens from Guizhou, South China, this species has been widely recognised in Late Permian to Early Triassic sequences of South China. As a result, this species has been considered to be one of the most common brachiopods of the Late Permian of the Tethyan Province (Liao 1987), and one of the characteristic elements of the so-called mixed Permian–Triassic boundary fauna in South China (Liao 1987). However, our review demonstrates that this species has been attributed to several different genera by various authors, including *Pugnax* Hall & Clarke (Huang 1933; Wang 1955; Wang et al. 1964; Jin & Liao 1974; Tong 1978; Feng & Jiang 1978; Zhan in Hou et al. 1979), *Neowellerella* Dagys (Jin et al. 1979; Liao 1979, 1980a, 1980b, 1981, 1982, 1984, 1987; Liao & Meng 1986; Zhan in Li et al. 1989), *Lissorhynchia* Yang & Xu (Xu in Yang et al. 1987) and *Prelissorhynchia* Xu & Grant (Xu & Grant 1994).

Huang (1933) did not fully describe the detailed internal features of the species, therefore leaving the generic position of the species open to interpretation. A broad definition of *Pugnax pseudoutah* Huang has been adopted by different authors, resulting in several unrelated specimens being referred to the species. For example the eastern Chinese specimens from the uppermost Permian to basal Triassic of Zhejiang and Fujian Provinces, described by Liao (1979, 1980a, 1980b, 1984), which possess a subpentagonal shape and a rather flat profile with a distinctive impression of a median ridge in the dorsal valve, belong to a distinct species. These specimens are different from others referred to the same species from Sichuan Province described by Xu (in Yang et al.

1987) and Xu & Grant (1994), in that the latter have a much thicker lateral profile, and are ornamented by rounded plicae, and lack a dorsal median ridge. In fact, both these collections are different from the type specimens of '*Pugnax*' *pseudoutah* Huang (1933: 64–66, pl. 10, figs 1–8) and belong to two separate species. *Pugnax pseudoutah* Huang is revised herein and placed in *Prelissorhynchia* Xu & Grant. However, the specimens, referred to *Prelissorhynchia pseudoutah* (Huang) by Xu & Grant (1994), are considered to represent a different species.

The specimens described in this paper were collected from the Huangzhishan section of Huzhou City, Zhejiang Province (Fig. 1, loc. 5) by the senior author in the summer of 1996. These specimens are externally closer to the type specimens of '*Pugnax*' *pseudoutah* Huang from Guizhou than any of the previously figured specimens under the same species name from elsewhere in South China. Comparison with the type specimens deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, was also undertaken for the present study.

STRATIGRAPHY OF THE NEW MATERIAL

The Huangzhishan section is located 30 km east of the Meishan section, Changxing, Zhejiang Province. This section has a continuous succession of marine Permian–Triassic boundary Beds (Fig. 2). The specimens were collected from Beds 11 and 12 of argillaceous limestones interbedded with mudstone (Fig. 2). The top of bed 12 is succeeded by a white clay bed, used extensively as a marker horizon for the Permian–Triassic boundary in South

China. Bed 12 itself is characterised by the appearance of a mixed fauna of Permian-like brachiopods and Triassic-like bivalves. Characteristic fusulinid species of the *Paleofusulina* Zone and conodont *Clarkina changxingensis* Zone occur lower in the section (Beds 1–2). Bed 10 yields the following brachiopods: *Peltichia* sp., *Paryphella orbicularis* Liao, *Leptodus nobilis* Waagen, *L. diminutus* Liao. Bed 11 is characterised by abundant brachiopods, including *Derbyia* sp., 'Waagenites' *quadrata* Zhan, 'W.' *longtanensis* Liao, 'W.' *soochowensis* Chao, *Lissochonetes* sp., *Neochonetes zhongyinensis* Liao, *N. convexa* Liao, *Chonetinella substrophomenoides* Huang, *Paryphella orbicularis* Liao, *P. triquetra* Liao, *Haydenella buravasi* Grant, *H. kiangsiensis* (Kayser),

Spinomarginifera alpha Huang, *S. kueichowensis* Huang, *S. chengyaoyensis* Huang, *Martinia* sp., *Crurithyris speciosa* Wang, *C. flabelliformis* Liao, *Uncinunellina* sp., *Prelissorhynchia pseudoutah* (Huang). Bed 12 contains the brachiopods *Acosarina strophiria* Xu., 'Waagenites' *pignaea* (Liao), 'W.' *quadrata* Zhan, *Spinomarginifera kueichowensis* Huang and *Prelissorhynchia* sp. Beds 13 and 14, a white clay bed and a black mudstone respectively, correlate with the White Clay bed (Bed 25) and Black Clay bed (Bed 26) of the Meishan section respectively. At Meishan, the currently widely accepted Permian–Triassic boundary is placed at the base of Bed 27b according to the evolutionary succession of conodonts (Yin 1994; Wang 1994). Therefore, the

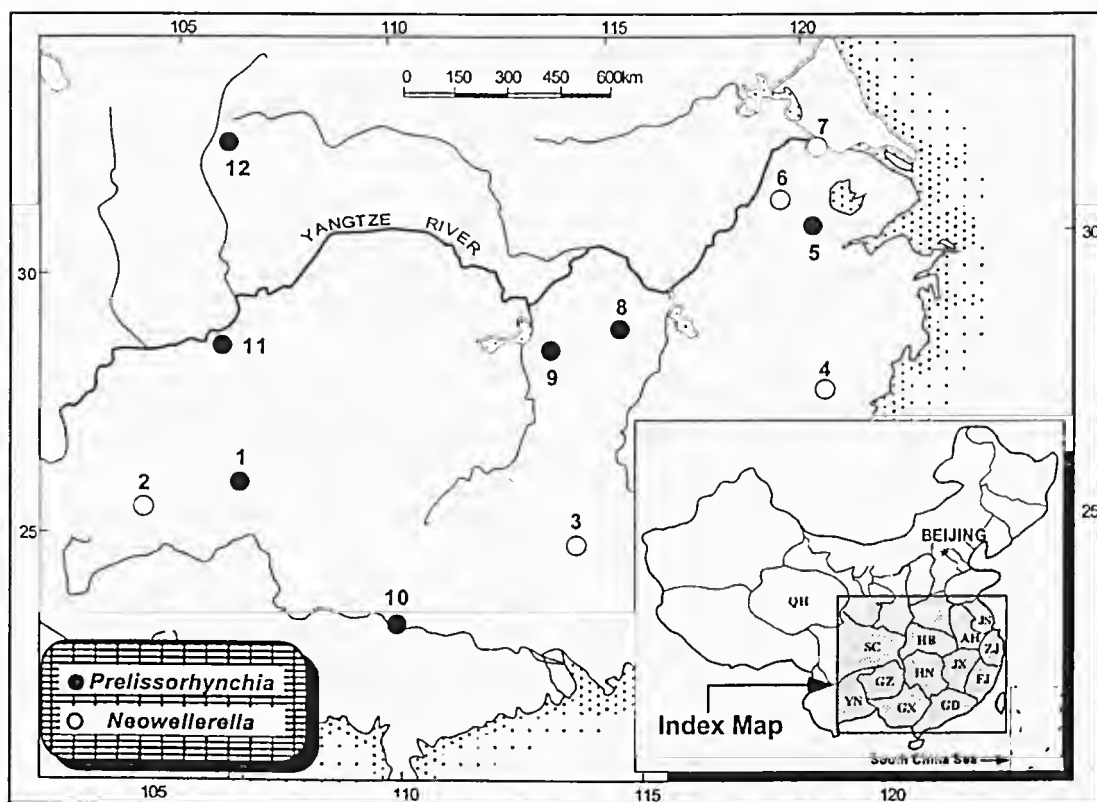


Fig. 1. The map showing the localities of *Prelissorhynchia* Xu & Grant (1994) and *Neowellerella* Dagens (1974) in South China. QH: Qinghai Province; SC: Sichuan Province; HB: Hubei Province; HN: Hunan Province; YN: Yunnan Province; GZ: Guizhou Province; GX: Guangxi Province; GD: Guangdong Province; JX: Jiangxi Province; FJ: Fujian Province; ZJ: Zhejiang Province; JS: Jiangsu Province; AH: Anhui Province. 1: Tatinghsien section, Anshuan County, GZ; 2: Zhongyin section, Qinglong County, GZ; 3: Shuizutang section, Lian County, GD; 4: Fushi section, Yongding County, FJ; 5: Huangzhishan Section, Huzhou City, ZJ; 6: Meishan section, Changxing County, ZJ; 7: Longtan section, Nanjing City, JS; 8: Huatang section, Chengxian County, HN; 9: Meitian section, Yizhang County, HN; 10: Matan section, Heshan City, GX; 11: Banzhuyuan section, Nantong County, SC; 12: Shangsi section, Guangyuan County, SC.

Permian-Triassic boundary at the Huanzhishan section should be drawn approximately at the top of the black mudstone (Bed 14) (Fig. 2). The following fossils, including the ammonoid *Ophiceras* sp., bivalve *Claraia* sp., and brachiopods *Lingula fuyuanensis* Liao and *Paracrurithyris pigmaea* Liao, are found in Beds 15-17. These elements are common in the Changhsingian and Griesbachian in South China.

The specimens studied and figured in this paper are deposited in the following institutions: the Nanjing Institute of Geology and Palaeontology, Academia Sinica, China (NIGP) and the Museum of Victoria, Melbourne (NMV).

Phylum BRACHIOPODA

Subphylum RHYNCHONELLIFORMEA Williams, Carlson, Brunton, Holmer & Popov, 1996

Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer & Popov, 1996

Order RHYNCHONELLIDA Kuhn, 1949

Suborder RHYNCHONELLIDINA Muir-Wood, 1955

Superfamily WELLERELLOIDEA Xu & Liu, 1983

Family PONTISIDAE Cooper & Grant, 1976

Genus *Prelissorhynchia* Xu & Grant, 1994
(emend herein)

Type species. *Pugnax pseudoutah* Huang, 1933.

Diagnosis. Small in size; subtriangular in outline, slightly wider than long; unequally biconvex; anterior commissure strongly uniplicate. Ventral valve slightly convex, with a pronounced sinus developed in anterior part; beak suberect or slightly incurved; deltidial plates open or covered by short deltidial plates. Dorsal valve strongly convex with a conspicuous median fold. Pliae angular, few and simple, separated by subangular valleys, originating at midvalve, and confined to the anterior part of the shell; two plicae within the sulcus, and three on the fold. Ventral interior with large knob-like teeth; dental plates strong and subparallel anteriorly. Dorsal interior with cardinal plate, erura falseifer-shaped; socket ridges strong, inclined over smooth sockets; inner hinge plate forming bridge, often convex (Fig. 3); median septum absent, but myophragm or thick secondary swelling well developed, serving median ridge anteriorly.

Comparison and discussion. *Neowellereella* Dagys (1974) shares dorsal internal features with the present genus, but is parasulcate at its anterior commissure and has fewer plicae near the anterior margin and much flattened shells.

Pontisia Cooper & Grant (1969) also develops very similar external and internal features like those of *Prelissorhynchia*, but differs in having somewhat flattened, rather than convex valves, rounded and longer but finer costae originating from near the beak, and an elongate-oval foramen. Internally, *Pontisia* has a pair of smaller teeth within the ventral interior.

Tautosia Cooper & Grant (1969) is generally transverse in outline, with a strong fold and a deep sulcus, and is usually paucicostate, therefore suggesting close resemblance to the present genus, but *Tautosia* has a strong median septum in the dorsal interior.

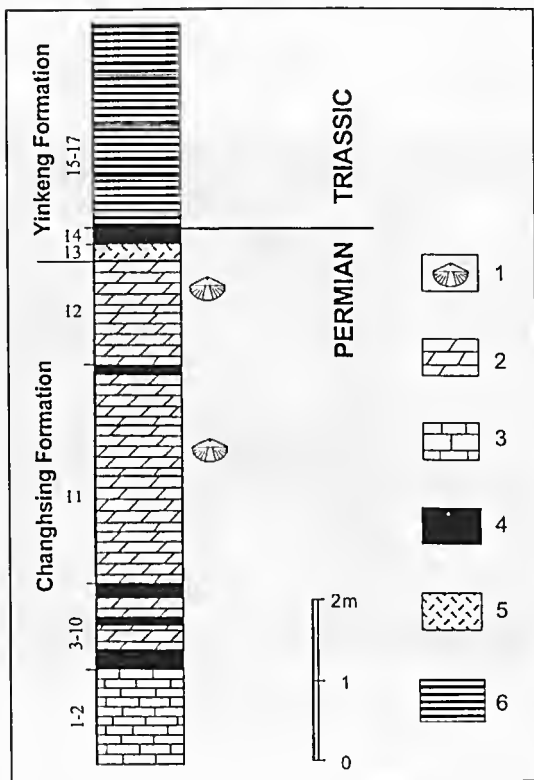


Fig. 2. The stratigraphic distribution of *Prelissorhynchia* Xu & Grant, 1994 in the Huangzhishan section. 1: *Prelissorhynchia* horizons; 2: argillaceous limestone; 3: limestone; 4: black shale; 5: white clay bed; 6: calcareous mudstone.

SYSTEMATIC PALAEONTOLOGY

The supra-ordinal classification follows the revision prepared for the new Treatise by Williams et al. (1996). All morphological terms are from Williams et al. (1965) and Brunton et al. (1996).

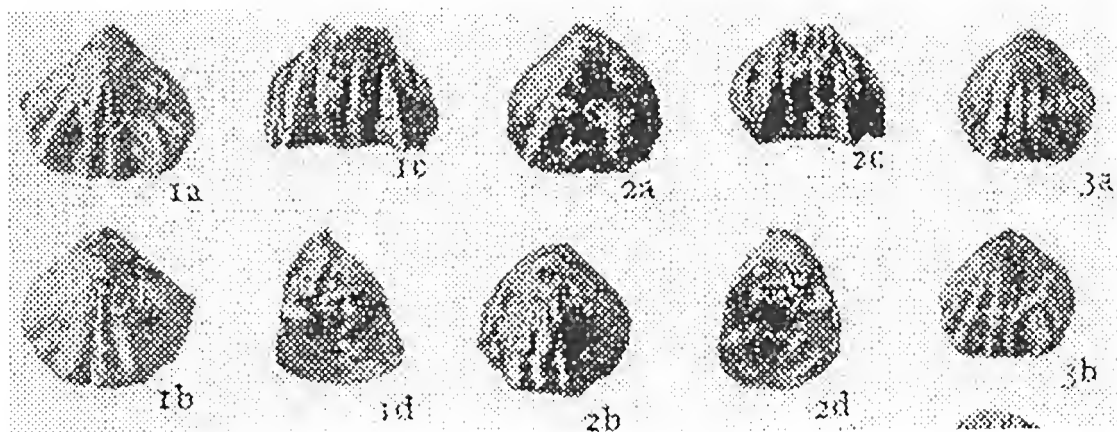


Fig. 3. The type specimens of *Prelissorhynchia pseudoutah* (Huang) from the Upper Permian of Guizhou Province, South China (after Huang 1933: 64–66, pl. 10, figs 1–3).

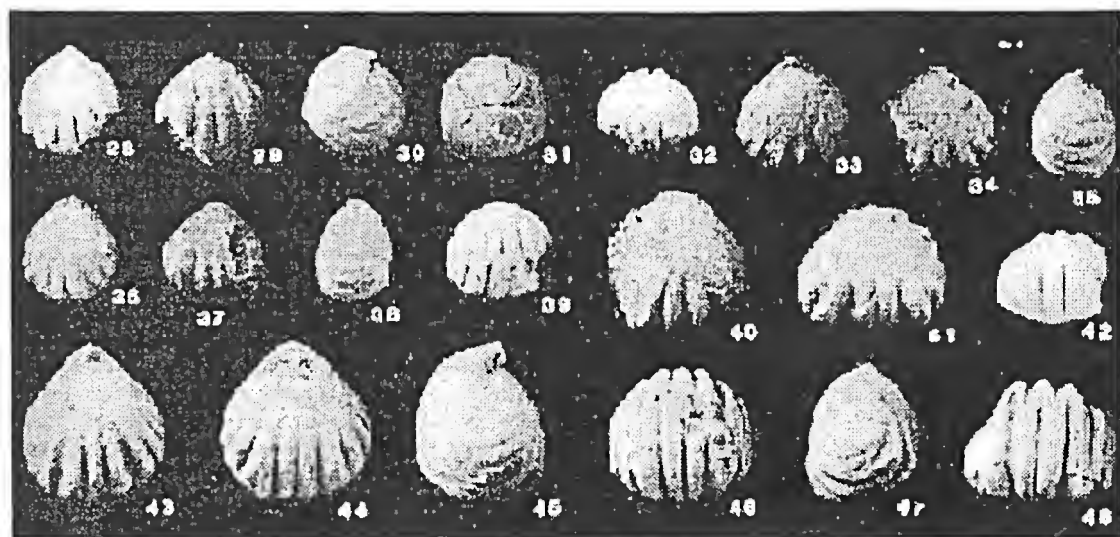


Fig. 4. The type specimens of *Prelissorhynchia xui* sp. nov. from the Upper Permian of the Baizhuyuan section of Nantong County, Sichuan Province, South China (after Xu & Grant 1994: 38, fig. 22: 28–48).

Externally, the present genus may be confused with *Pugnax* Hall & Clarke (1893) with which it shares many external features. However, *Pugnax* possesses separated hinge plates and the crura are supported by crural plates. In contrast, *Prelissorhynchia* has relatively longer, crescentic crura, and lacks a median septum in both valves. The present genus is also externally close to the Triassic genus *Rhyuchonella* Fischer de Waldheim (1809), especially in outline and pattern of plication, but the latter is characterised by a dorsal septalium supported by a low median septum.

More recently, Xu (in Yang et al. 1987) allied the species name *pseudoutah* to the specimens from Hunan Province (Fig. 1, loc. 9), and referred the species to *Lissorhynchia* Yang & Xu (1966). Later, Xu & Grant (1994) erected a new genus, *Prelissorhynchia*, for material from Sichuan Province and they nominated *Pugnax pseudoutah* Huang as the type species. In the same paper, Xu & Grant assigned specimens from the Banzhuyuan section of Sichuan Province (Fig. 1, loc. 11) to *Prelissorhynchia pseudoutah*. The Sichuan and Hunan material (Fig. 4), as figured by Xu (in Yang

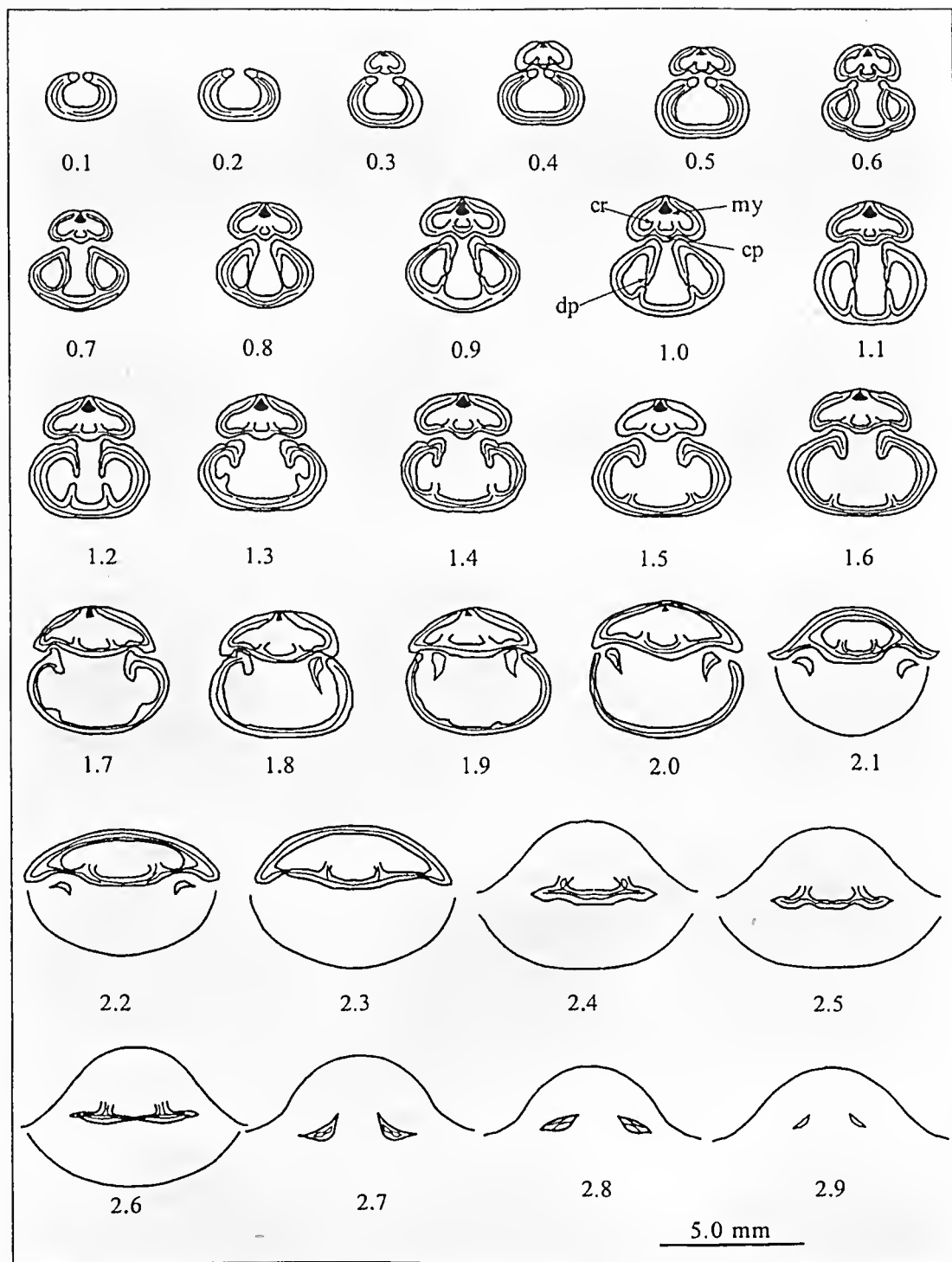


Fig. 5. Serial sections of *Prelissorhynchia pseudoutah* (Huang) (based on specimens NMV P149268), showing the internal features. The numbers are the distance from the beak, the orientation of the sections is with ventral valve down, the below horizontal line represents the scale. dp: dental plates; cp: cardinal plate; cr: crura; my: myophragm.

et al. 1987) and Xu & Grant (1994) respectively, is significantly different from the type specimens (Fig. 5) of '*Pugnax*' *pseudoutah* from Guizhou Province as originally described and figured by Huang (1933), in that they appear to represent two mutually distinguishable species. Consequently, the specific assignment of these specimens described by Xu & Grant (1994) is questionable. For these reasons, the diagnosis of the genus, *Preliissorhynchia* Xu & Grant, is emended herein based on a careful examination of our collection and the type specimens of Huang's species, housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The low but distinctive myophragm is observed in the dorsal interior of *Preliissorhynchia* Xu & Grant.

Some specimens hitherto named *Neowellerella pseudoutah* (Huang) by Liao (1979, 1980a, 1980b, 1984) are also distinguishable from typical '*Pugnax*' *pseudoutah* Huang (1933). These specimens are revised below.

Preliissorhynchia pseudoutah (Huang, 1933)

Fig. 6A–F, H–J, L–R

Pugnax pseudoutah Huang 1933: 64–66, pl. 10, figs 1–8.—Wang 1955: 134, pl. 73, figs 13–16.—Wang et al. 1964: 396–397, pl. 66, figs 12–15.—Jin & Liao 1974: 312, pl. 165, figs 7–9.—Feng & Jiang 1978: 272, pl. 101, fig. 3.

Neowellerella pseudoutah.—Liao & Meng 1986: pl. 4, fig. 7.—Liao 1987: 108, pl. 5, fig. 29; pl. 8, fig. 1.

Lectotype. *Pugnax pseudoutah* Huang, 1933: 64–66, pl. 10, figs 1a–d. A specimen (Cat. 4728a) with two valves conjoined from the coal-bearing beds (Lungtan Formation; Wuchiapingian) of Jiazishan section of Anshuan County, Guizhou Province (Fig. 1, loc. 1), kept in the Nanjing Institute of Geology and Palaeontology, Academia Sinica (selected herein).

Discussion. When Huang (1933) first described the species, he figured three specimens (NIGP 4728a–c) as syntypes without designating a holotype. Among these syntypes, specimen NIGP 4728a is most clearly illustrated and is selected herein as the lectotype of *Preliissorhynchia pseudoutah* (Huang).

Xu & Grant (1994) and previous authors did not select a lectotype for the species.

Material. Twenty-five articulated shells from Bed 11 of the Changhsing Formation of the Huangzhishan section (Fig. 2) were studied. Of these, six are figured herein (NIGP 130585–90); NMV P149267–9 were serially sectioned in order to study the internal features.

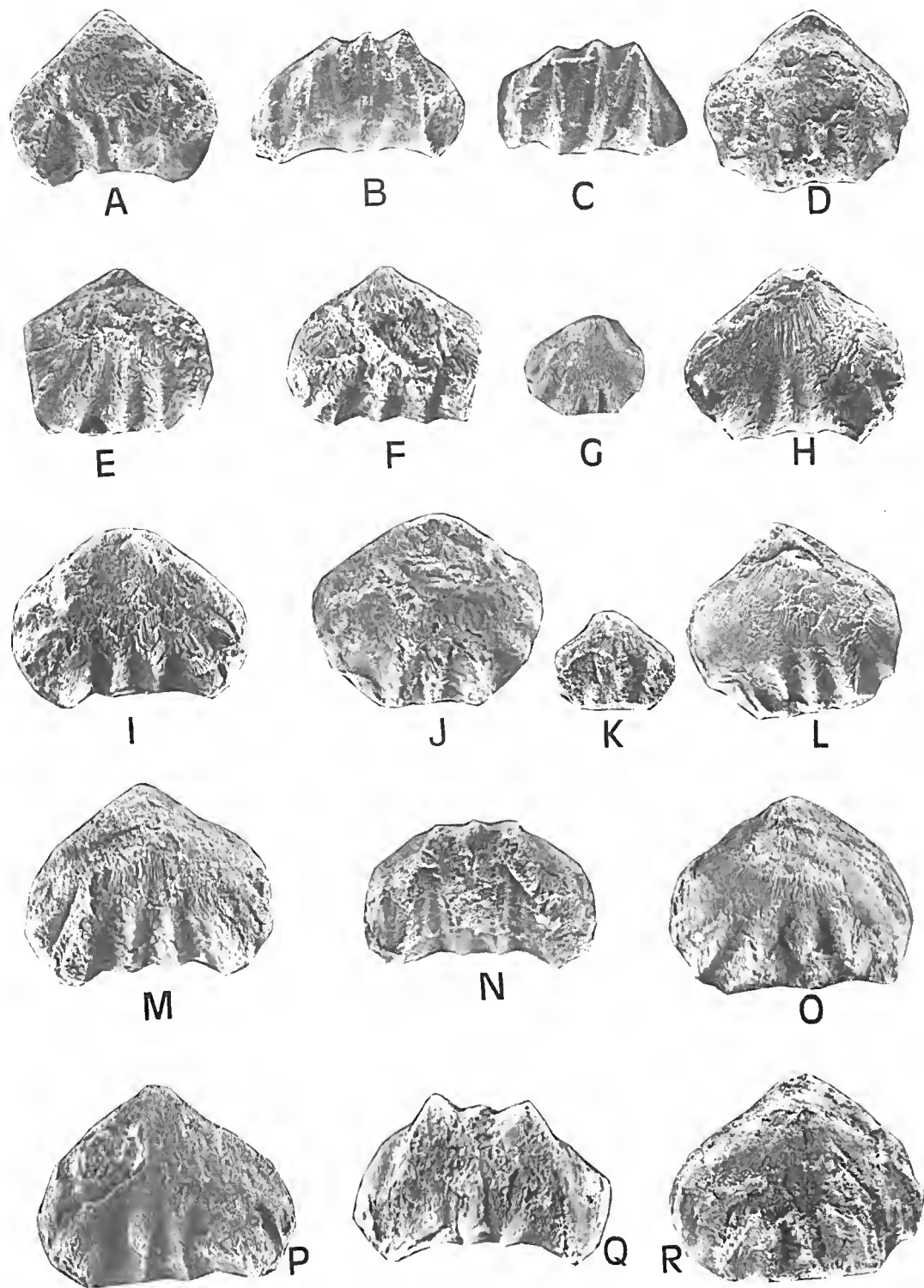
Measurements (in mm)

Specimen	Width	Length	Thickness	Apical angle
NIGP 130585	6.5	5.0	6.0	95°
NIGP 130586	6.8	5.0	6.5	105°
NIGP 130587	6.0	4.8	5.8	112°
NIGP 130588	7.0	5.8	7.0	115°
NIGP 130589	7.0	6.0	7.0	117°
NIGP 130590	7.8	6.2	7.1	113°
NMV P149267	7.0	5.0	5.5	95°
NMV P149268	7.0	6.0	5.0	112°
NMV P149269	6.0	5.0	5.0	108°

Diagnosis. Small-sized *Preliissorhynchia*; outline roundly to transversely triangular; unequally biconvex; profile narrowly subtriangular; anterior commissure strongly uniplicate; dorsal fold beginning at midvalve, furnished with three plicae; ventral sulcus deep, originating at midvalve, ornamented by two plicae. Ventral interior with strong and large knob-like teeth; dental plates strong and subparallel anteriorly, extending to about midvalve. Dorsal interior with cardinal plate; crura falcifer-shaped; socket ridges strong and high; inner hinge plate forming bridge, often convex; median septum absent, but myophragm or thick secondary swelling well developed, serving median ridge anteriorly.

Description. Shell very small (see measurements above); outline roundly to transversely triangular; unequally biconvex, dorsal valve more convex than ventral valve; apical angle between 95–117°; profile narrowly subtriangular; anterior commissure strongly uniplicate; dorsal fold beginning at midvalve, increasing in height to anterior margin, profile of fold strongly convex; ventral sulcus deep, originating at midvalve.

Fig. 6. A–F, H–J, L–R, *Preliissorhynchia pseudoutah* (Huang). A, D, NIGP 130585, ventral and dorsal views; B, H, L, NIGP 130586, anterior, ventral and dorsal views; C, E, F, NIGP 130587, dorsal and ventral views; I, J, NIGP 130588, ventral and dorsal views; M, N, O, NIGP 130589, ventral, anterior and dorsal views; P, Q, R, NIGP 130590, ventral, anterior and dorsal views. All $\times 5$. G, K, *Preliissorhynchia* sp., NIGP 130595, ventral and dorsal views. All $\times 3$. All specimens come from the top of Changhsing Formation of Huangzhishan Section, Huzhou, Zhejiang (Fig. 1, loc. 5).



Ventral valve slightly inflated posteriorly, becoming broadly and gently concave anteriorly; flanks slightly to strongly reflexed, lateral profile gently convex; beak well pointed, slightly incurved, and slightly elevated above dorsal beak; foramen small and triangular. Dorsal valve strongly convex from beak to anterior margin, umbo slightly flattened; apex concealed by ventral beak, covered by delthyrium; flanks moderately convex.

External surface of shells ornamented by about 6–7 simple plicae, originating at midvalves, confined to anterior part of shell, crests angular, separated by subangular valleys; fold with three angular plicae, separated by two deep valleys corresponding to the two plicae of sulcus; two low and sometimes ill defined plicae present on each flank; anterior commissure typically W-shaped. External surface of shells marked by very fine, irregular radial striations.

Ventral interior with strong and large knob-like teeth; dental plates strong and subparallel anteriorly, extending to about midvalve. Dorsal interior with cardinal plate; crura falcifer-shaped; socket ridges strong and high, inclined over smooth sockets; inner hinge plate forming bridge, often convex; median septum absent, but myophragm or thick secondary swelling well developed, serving median ridge anteriorly (Fig. 5).

Discussion. Our specimens (Fig. 6) are comparable with the type specimens (Fig. 3) of *Prelissorhynchia pseudoutah* (Huang 1933) in most aspects. Hence, we refer these specimens to *P. pseudoutah*. This species is described and illustrated herein because of the lack of details in Huang's (1933) original description. Although the species name *pseudoutah* has been variably applied to specimens from many different South Chinese faunas, some of these specimens can be readily discriminated from the type specimens figured herein (Fig. 3), and also figured by Huang (1933: pl. 10, figs 1–8).

Tong (1978: 241–242, pl. 85, figs 11a–c) described and figured a specimen as *Pugnax pseudoutah* from the Changhsingian of the Yakou section of Puzimiao, Pengshui County, Sichuan, but this specimen possesses divided hinge plates in the dorsal interior, unlike the undivided hinge plate of *Prelissorhynchia pseudoutah*. Therefore, it is probably a new species of *Pugnax* Hall & Clarke rather than a *Prelissorhynchia*.

Jin et al. (1979: 105, pl. 30, figs 6–9) figured several specimens as *Neowellerella* cf. *pseudoutah* (Huang). These specimens possess similar external features to Huang's material, but lack dental plates in the ventral interior and convex inner hinge

plates in the dorsal interior, indicating significant differences from Huang's species. These specimens probably represent a new genus of Wellerellidae.

Zhan (in Hou et al. 1979: 95, pl. 8, figs 21–22) described and figured a specimen from the Shuizutang section of Lian County of northern Guangdong Province (Fig. 1, loc. 3) under the name of *Pugnax pseudoutah* Huang. The Guangdong specimen possesses longer, rounded costae within the sulcus, and is also different from typical *Prelissorhynchia pseudoutah* (Huang) in having an elongate triangular outline. The Guangdong material is probably a species of either the *Stenosclimatidae* or *Neowellerella*.

Liao (1979: pl. 1, fig. 11; 1980a: pl. 1, figs 10–11; 1982: 235, pl. 96, figs 18–19; 1984: pl. 2, fig. 24) figured several specimens as *Neowellerella pseudoutah* (Huang) from the Early Triassic Yinkeng Formation of the Meishan section of Changxing, Zhejiang Province (Fig. 1, loc. 6), also from the Late Permian Talung Formation of Yongding, Fujian Province (Fig. 1, loc. 4), and from the Longtan section of Nanjing, Jiangsu Province (Fig. 1, loc. 7). Liao's specimens possess a subpentagonal outline and low convexity in both valves. The ventral sulcus originates at the beak, and bears two weak plicae separated by a weak shallow median trough. These features show that these eastern Chinese brachiopods are very different from the typical specimens of *Prelissorhynchia pseudoutah* (Huang); they probably belong to a new species of either *Neowellerella* Dagys or *Prelissorhynchia* Xu & Grant depending on their internal features.

The Changhsingian specimen of the Zhongyin section in Qinglong County of Guizhou Province (Fig. 1, loc. 2), also named as *N. pseudoutah* (Huang) by Liao (1980a: pl. 2, figs 1–2; 1980b: pl. 7, figs 38–39), has low convexity in both valves and concentric lamellae on the anterior of the umbonal region, unlike the lectotype of this species. On the other hand, this Guizhou specimen resembles and may prove to be conspecific with some eastern Chinese specimens figured by Liao (1979, 1980a, 1980b, 1984) as discussed above. It is worthy noting that both the specimens from eastern China and Guizhou figured by Liao are readily distinguishable from *Prelissorhynchia pseudoutah* of Xu & Grant (1994: 38, fig. 22: 28–48) in having a low convex profile and weak plicae on both valves.

Specimens referred to as *Lissorhynchia pseudoutah* (Huang) by Xu (in Yang et al. 1987: 229, pl. 13, figs 15–16; pl. 14, figs 10–12) and as '*Prelissorhynchia pseudoutah* (Huang)' by Xu & Grant (1994) are both very different from the type

material of *Preliissorhynchia pseudoutah* (Huang). These specimens represent two distinct genera as correctly and appropriately named by Xu (in Yang et al. 1987) as *Lissorhynchia* and by Xu & Grant (1994) as *Preliissorhynchia*. However, they are unable to be referred to as *Preliissorhynchia 'pseudoutah'* (Huang), which is herein renamed *Preliissorhynchia xui* sp. nov. (see next) (Table 1).

Neowellerella pseudoutah of Zhan (in Li et al. 1989: pl. 26, figs 9–11) from the Late Permian Talung Formation of the Shangsi section in Guangyuan, Sichuan (Fig. 1, loc. 12) is less inflated in profile and has low, rounded costae, a shallow median sulcus and low median fold, suggesting resemblance to the Sichuan specimens of Xu & Grant (1994) rather than to Huang's type material of *Preliissorhynchia pseudoutah*.

The Hunan specimens from the Huatang section of Chengxian County (Fig. 1, loc. 8) (Liao & Meng 1986: pl. 4, fig. 7) and the siliceous specimens from the Late Permian Talung Formation of the Matan section of Laibin, Guangxi (Fig. 1, loc. 10) (Liao 1987: 108, pl. 5, fig. 29; pl. 8, fig. 1) seem to be referable to *Preliissorhynchia pseudoutah* (Huang) as described herein because they all have similar external and internal features.

Waterhouse (1983: 131–132, pl. 4, figs 4–5) also compared Huang's species with specimens from Thailand. The Thai species has longer and more flattened valves, and is perhaps more closely related to a member of *Stenoscismatidina*, as also suggested by Waterhouse.

In summary, specimens previously assigned to '*Pugnax pseudoutah*' Huang from the Late Permian to the Early Triassic of South China can be approximately referred to three separate taxa (Table 1). The material from Guizhou (Huang 1933; Wang 1955; Wang et al. 1964; Jin & Liao 1974; Feng & Jiang 1978), Hunan (Liao & Meng 1986), Guangxi (Liao 1987), and the specimens described herein from Zhejiang are considered to be conspecific with Huang's (1933) original specimens. The specimens from the mixed beds of the Permian–Triassic boundary of Jiangsu, Zhejiang and Fujian Provinces (Liao 1979, 1980a: pl. 1, figs 10–11; 1981, 1984) and Guizhou (Liao 1980a: pl. 2, figs 1–2; 1980b) represent a new species, but its generic position is indeterminable due to poor knowledge of the internal structures. The Sichuan material figured by Xu (1987), Zhan (1989), Xu & Grant (1994) is assigned to *Preliissorhynchia xui* sp. nov. The specimen from the Changhsingian of the Yakou section of Puzimiao, Peshui County, Sichuan Province (Tong 1978: 241–241, pl. 85, figs 11a–c) probably represents a new species of *Pugnax* Hall & Clarke. The Qinghai material

figured and studied by Jin et al. (1979) is probably a new species of a new genus of the Wellerellidae.

Preliissorhynchia sp.

Fig. 6G, K

Material. NIGP 130595, one complete specimen with two valves conjoined from bed 12 of the Huangzhishan section, Huzhou City, Zhejiang Province.

Measurements (in mm). Maximum width: 5.5; length: 3.9; thickness: 4.8; apical angle: 108°.

Description. Small in size; subtriangular in outline; unqually biconvex, greatest width near anterior of shell; postero-lateral margins gently concave; anterior margin truncate, anterior commissure uniplicate; median sulcus and fold pronounced, originating at midvalve. Surface semicostate, costae strong and distinct, beginning at midvalve; three costae on fold, two in sulcus.

Ventral valve moderately convex; gently convex in lateral profile but deeply concave in anterior profile; median sulcus deep; flanks narrow, concave, with costae. Dorsal valve strongly convex in lateral profile, more inflated than ventral valve with greatest convexity near anterior margin; anterior profile strongly domed with gently rounded top but steep flanks. Fold highly convex; flanks depressed and narrowly rounded. Internal structures unknown.

Discussion. This specimen is indicative of another species of *Preliissorhynchia* in the present collection. It is comparable to *H. pseudoutah* (Huang), but differs in having rather compressed valves and a deeply concave, broadly rounded postero-lateral margin in the dorsal valve. This specimen is also different from the material from Fujian, Zhejiang and Jiangsu Provinces studied by Liao (1979, 1980b, 1984) in possessing a deep sulcus with conspicuous median plicae. It is likely that the present specimen represents a new species.

Preliissorhynchia xui sp. nov.

Fig. 4

Lissorhynchia pseudoutah (Huang).—Xu in Yang et al. 1987: 229, pl. 13, figs 15–16; pl. 14, figs 21–22.

Preliissorhynchia pseudoutah (Huang).—Xu & Grant 1994: 38, fig. 22: 28–48; fig. 23.

Holotype. Figured by Xu & Grant 1994: 38, fig. 22: 43–46. A specimen (USNM 456064b) with two valves conjoined from the Late Permian deposits of Baizhuoyuan section of Nantong, Sichuan Province (Fig. 1, loc. 11), kept in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Species	Age	Locality (see Fig. 1)	Author	Revised herein
<i>Pugnax pseudoutah</i> Huang	Changhsingian	GZ	Huang (1933) Wang (1955) Wang et al. (1964) Jin and Liao (1974) Feng and Jiang (1978)	<i>Prelissorhynchia pseudoutah</i> (Huang)
<i>Neowellerella pseudoutah</i> (Huang)	Changhsingian	HN	Liao and Meng (1986)	
<i>N. pseudoutah</i> (Huang)	Changhsingian to Early Triassic	GX	Liao (1987)	
<i>Lissorhynchia pseudoutah</i> (Huang)	Changhsingian	HN	Xu (1987)	<i>Prelissorhynchia xui</i> sp. nov.
<i>N. pseudoutah</i> (Huang)	Changhsingian	SC	Zhan (1989)	
<i>Prelissorhynchia pseudoutah</i> (Huang)	Changhsingian	SC	Xu and Grant (1994)	
<i>N. pseudoutah</i> (Huang)	Changhsingian	GZ	Liao (1980a,b)	? <i>Neowellerella</i> sp.
<i>N. pseudoutah</i> (Huang)	Changhsingian to Early Triassic	ZJ FJ JS	Liao (1979, 1980a) Zhao et al. (1981) Wang et al. (1982) Liao (1984)	
<i>Pugnax pseudoutah</i> Huang	Changhsingian	GD	Zhan (1979)	
<i>Pugnax pseudoutah</i> Huang	Changhsingian	SC	Tong (1978)	? <i>Pugnax</i> sp.
<i>Neowellerella</i> cf. <i>pseudoutah</i> (Huang)	Late Permian	QH	Jin et al. (1979)	? ??

Table 1. Revision of species referred to *pseudoutah* Huang from the Late Permian to Early Triassic in South China.

Diagnosis. Small, subtriangular to subcircular, thick in lateral profile, semicostate, sulcus and fold commencing from somewhat anterior to midlength, costae rounded, 2 in sulcus, 3 on fold, 2–3 on each lateral side. Ventral interior with large, knob-like teeth; dental plates strong and subparallel extended. Dorsal interior with undivided hinge plate, but hinge plates separating socket ridges and crural bases, inner hinge plates forming arched bridge; sockets shallow, socket ridges low; crura crescentic; median septum absent.

Discussion. The detailed description has been provided by Xu & Grant (1994: 38, fig. 22: 28–48; fig. 23). The new species is similar to *Prelissorhynchia pseudotai* (Huang) in both external and internal features, but is easily separated from the latter by a subcircular outline with a greater shell thickness, higher shell convexity, and rounded plications. The low but distinctive myophragm is present at the dorsal interior of *Prelissorhynchia pseudotai* (Huang) (Fig. 5), but appears to be absent in the new species (Xu & Grant 1994: 38, fig. 23).

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REFERENCES

- BRUNTON, C. H. C., LAZAREV, F. & MACKINNON, D. I., 1996. Morphological Terms used to describe the Cardinalia of Articulate Brachiopods: Homologies and Recommendations. *Historical Biology* 11: 9–41.
- COOPER, G. A. & GRANT, R. E., 1969. New Permian brachiopods from West Texas, 1. *Smithsonian Contributions to Paleobiology* 1: 1–20, 5 pls.
- COOPER, G. A. & GRANT, R. E., 1976. Permian brachiopods of West Texas, 5. *Smithsonian Contributions to Paleobiology* 24: 2609–3159, 117 pls.
- DAGYS, A. S., 1974. Triasovye Brachiopody (Morfologiya, Sistema, Filogeniya, Stratigraficheskoe Znachenie i Biogeografiya) [Triassic Brachiopoda (Morphology, Systematics, Phylogeny, Stratigraphic Distribution and Biogeography)]. *Akademiya Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Trudy* 214: 1–386, 49 pls. [In Russian.]
- FENG, R. L. & JIANG, Z. L., 1978. Brachiopoda. In *Palaeontological Atlas of Southwestern China, Guizhou Province* 2: 231–304, pls 85–108. Geological Publishing House, Beijing. [In Chinese.]
- FISCHER DE WALDHEIM, G., 1809. Notice des fossiles du gouvernement de Moscou. Partie I. Sur les coquilles fossiles dites terebratules. *Invitation a la Seance publique de la Societe imperiale des naturalistes de Moscou*, 1–35, 3 pls. [In Russian.]
- GRANT, R. E., 1970. Brachiopods from Permian–Triassic boundary beds and age of Chhidru Formation, West Pakistan. In *Stratigraphic boundary problem: Permian and Triassic of West Pakistan*, B. Kummel & C. Teichert, eds, Kansas University Press, *Special Publication* 4: 117–151, 71 pls.
- HALL, J. & CLARKE, J. M., 1893. An Introduction to the Study of the genera of Palaeozoic Brachiopoda. *New York Geological Survey, Palaeontology (Albany)* 8(2): 1–317, pls 21–84.
- HUANG, T. K., 1933. Late Permian brachiopods of Southwestern China, Part 2. *Geological Survey of China, Palaeontologica Sinica, Series B* 9(2): 1–172, 11 pls.
- JIN, Y. G. & LIAO, Z. T., 1974. Carboniferous and Permian brachiopods. In *A Handbook of the Stratigraphy and Palaeontology in Southwest China*, Nanjing Institute of Palaeontology and Geology, Academia Sinica. Science Press, Beijing, 275–282, pls 142–147; 308–313, pls 162–165. [In Chinese.]
- JIN, Y. G., SUN, D. L., XU, H. K. & YE, S. L., 1979. Brachiopoda. In *Palaeontological Atlas of North-western China, Qinghai Province*, Geological Publishing House, Beijing, 60–225, pls 18–57. [In Chinese.]
- LIAO, Z. T., 1979. Brachiopod Assemblage Zones of Changhsingian Stage and Brachiopods of the Mixed Fauna in South China. *Journal of Stratigraphy* 3(3): 200–213, 1 pl. [In Chinese.]
- LIAO, Z. T., 1980a. Upper Permian Brachiopods from Western Guizhou. In *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan*, Nanjing Institute of Geology and Palaeontology, Academia Sinica. Science Press, Beijing, 241–277, 9 pls. [In Chinese.]
- LIAO, Z. T., 1980b. Brachiopod Assemblages from the Upper Permian and Permian–Triassic Boundary beds, South China. *Canadian Journal of Earth Sciences* 17(2): 289–295, 2 pls.
- LIAO, Z. T., 1981. The new genera and species of brachiopods. In *The Changhsingian and Permian–Triassic Boundary of South China*, J. K. Zhao, J. Z. Sheng, Z. Q. Yao, X. L. Liang, C. C. Chen, L. Rui & Z. T. Liao, eds, *Bulletin, Nanjing Institute of Geology and Palaeontology, Academia Sinica* 2: 1–95. [In Chinese.]

- LIAO, Z. T., 1984. New genera and species of Late Permian and Earliest Triassic brachiopods from Jiangsu, Zhejiang and Anhui Provinces. *Acta Palaeontologica Sinica* 23(3): 276–285, 2 pls. [In Chinese with English abstract.]
- LIAO, Z. T., 1987. Palaeoecological characters and stratigraphic significance of silicified brachiopods of the Upper Permian from Heshan, Laibin, Guangxi. In *Stratigraphy and Palaeontology of Systemic Boundaries in China, Permian and Triassic Boundary*, Nanjing Institute of Geology and Palaeontology, Academia Sinica. Nanjing University Press, Nanjing, 81–125, 8 pls. [In Chinese with English abstract.]
- LIAO, Z. T. & MENG, F. Y., 1986. Late Changhsingian brachiopods from Huatang of Chengxian County, Southern Hunan. *Memoir of Nanjing Institute of Geology and Palaeontology, Academia Sinica* 22: 71–94, 5 pls. [In Chinese with English abstract.]
- TONG, Z. X., 1978. Permian and Carboniferous brachiopods. In *Palaeontological Atlas of Southwestern China, Sichuan Province*, Geological Publishing House, Beijing, 210–267, pls 77–92. [In Chinese.]
- WANG, C. Y., 1994. A conodont-based high-resolution eventostratigraphy and biostratigraphy for the Permian–Triassic boundaries in South China. *Palaeoworld* 4: 234–248, 1 pl.
- WANG, Y., 1955. Phylum Brachiopoda. In *Index Fossils of China*, Nanjing Institute of Geology and Palaeontology, Academia Sinica. Science Press, Beijing, 109–171. [In Chinese.]
- WANG, Y., JIN, Y. G. & FANG, D. W., 1964. *Brachiopod fossils of China* (2 vols). Science Press, Beijing, 1–777, 136 pls. [In Chinese.]
- WANG, G. P., LIU, Q. Z., JIN, Y. G., HU, S. Z., LIANG, W. P. & LIAO, Z. T., 1982. Brachiopods. In *Palaeontological Atlas of Eastern China*, Nanjing Institute of Mineralogy and Resources, Geologica Academia Sinica, ed., Geological Publishing House, Beijing, 186–250, pls 74–102. [In Chinese.]
- WATERHOUSE, J. B., 1983. A Late Permian Lytoniid fauna from northwestern Thailand. *Papers, Department of Geology, University of Queensland* 10(3): 111–153, 6 pls.
- WILLIAMS, A. & ROWELL, A. J., 1965. Morphological terms applied to Brachiopods. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda*, R. C. Moore, ed., H139–H155. Geological Society of America and University of Kansas Press, New York and Lawrence.
- WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. & POPOV, L., 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London, Series B* 351: 1171–1193.
- XU, G. R. & GRANT, R. E., 1994. Brachiopods near the Permian–Triassic boundary in South China. *Smithsonian Contributions to Paleobiology* 76: 1–65.
- YANG, Z. Y. & XU, G. R., 1966. *Triassic brachiopods of central Guizhou Province, China*. Geological Publishing House, Beijing, 1–151, 14 pls. [In Chinese.]
- XU, G. R., 1987. Brachiopoda. In *Permian–Triassic boundary stratigraphy and fauna of South China*, Z. Y. Yang, H. F. Yin, S. B. Wu, F. Q. Yang, M. H. Ding & G. R. Xu, eds, *Geological Memoir, Series 2 (Stratigraphy and Palaeontology)* 6: 317–326, pls 7–16, Geological Publishing House, Beijing. [In Chinese with English abstract.]
- YIN, H. F., 1994. Reassessment of the index fossils at the Paleozoic–Mesozoic boundary. *Palaeoworld* 4: 153–171.
- ZHAN, L. P., 1979. Brachiopoda. In *The coal-bearing strata and fossils of Late Permian from Guangdong*, H. F. Hou, B. W. Chen, L. P. Zhan, X. F. Zhu, Z. T. Gui & Sheng, H. G., eds, Geological Publishing House, Beijing, 61–100, pls 4–13. [In Chinese.]
- ZHAN, L. P., 1989. Brachiopoda. In *Study on the Permian–Triassic Biostratigraphy and Event Stratigraphy of Northern Sichuan and Southern Shaanxi*, Z. S. Li, L. P. Zhan, J. Y. Dai, R. G. Jin, X. F. Zhu, J. H. Zhang, H. Q. Huang, D. Y. Xu, Z. Yan & H. M. Li et al., eds, *Geological Memoirs, People's Republic of China, Ministry of Geology and Mineral Resources, Series 2* 9: 205–211, pls 25–28, Geological Publishing House, Beijing. [In Chinese with English abstract.]

GEOMORPHOLOGY OF THE HATTAH LAKES REGION ON THE RIVER MURRAY, SOUTHEASTERN AUSTRALIA: A RECORD OF LATE QUATERNARY CLIMATE CHANGE

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The Hattah Lakes series of interconnected lakes formed in a depression in the Mallee country on the River Murray. Several of these lakes lie on the floor of a pre-existing palaeo-lake, named here the Hattah Mega-Lake, which is bordered to the east by a large lunette. The rest lie on terraced floodplain sediments of the ancestral River Murray.

In this landscape three stages of fluvial, lacustrine and aeolian activity have been identified: (1) a pre-glacial stage of high river discharge and high lake water levels filling the Hattah Mega-Lake; (2) a glacial maximum stage of variable river discharge, with water levels higher than present but also encompassing periods of drought with low river levels and low water levels, and occasional drying of the mega-lake, accompanied by increased salinity, pelletal clay deflation and widespread aeolian activity; and (3) a post-glacial stage of low river discharge with vegetated floodplains, and low lake levels within smaller freshwater basin lakes.

THE geomorphology and Late Quaternary geological history of the Hattah Lakes, situated on the River Murray within the Hattah-Kulkyne National Park and Murray-Kulkyne Park, approximately 65 km south of Mildura (Fig. 1) is described in this study. They are one of the few wetland systems located on the margin of the River Murray within the semi-arid Mallee country of the western Murray Basin. In total there are about 21 lakes, all interconnected and filled by flooding of the River Murray by Chalka Creek, an anabranch that flows for approximately 18 km from its inlet to the lake system, and 26 km from the lakes back to its outlet (Fig. 2). The southern chain of lakes lie within the Hattah Lakes National Park, whereas the remainder are within the Kulkyne National Park and the Murray-Kulkyne Park along the River Murray.

The lakes are highly dependent on flooding of the River Murray, as the regional climate can be broadly classified as semi-arid with mean annual potential evaporation far exceeding median annual rainfall (Colls & Whitaker 1990). The record of river and lake levels, going back to 1908, indicates that the lake system is replenished by the River Murray once every two years, and has completely dried out only seven times between 1908 and 1964, the longest period being 24 months following the drought years 1943–45 (Robinson 1965). Observations made during the 1964 flood indicate

that all the lakes had filled when water levels reached 13 feet (42.96 AHD) in Lake Hattah (Robinson 1965).

Previous investigations of the region have been directed towards hydrology and ecology. The natural water regime of the lakes has been described (Robinson 1966) and the effects of river regulation on the lake system have been discussed (Robinson 1966; Baker & Wright 1978; Shaw 1985). Robinson (1965) suggested that the lakes were the remnant of a former course of the River Murray, and recognised that their shapes were strongly influenced by wind-blown sand ridges from the west. The only geological study of the area, conducted as part of a regional hydro-geological investigation of the River Murray (Thorne et al. 1991), noted the large extent of floodplain sediments overlain by dune sands in the Hattah Lakes area, and identified a large sandy lunette with the lake-floor now occupied by the Hattah Lakes. However, the relationship between the current lake system and the former one, and between the present and past fluvial systems of the River Murray was not investigated.

This paper describes the landforms in the Hattah Lakes area, including the fluvial sequence on the floodplains of the River Murray to the east, this leading to a discussion of the evolution of the region and implications for regional climatic and environmental change.

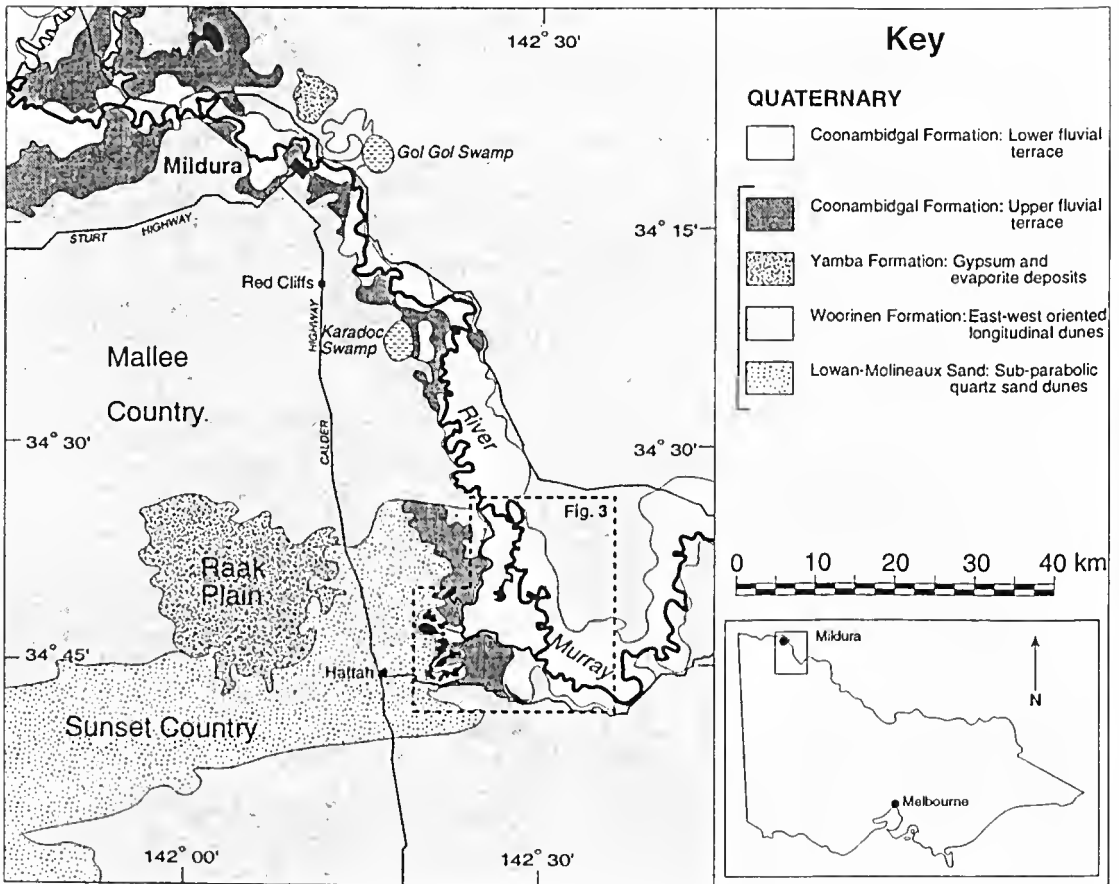


Fig. 1. Regional geology of northwestern Victoria, showing study area. Simplified after Lawrence (1972) and Lawrence & Macumber (1974).

REGIONAL SETTING OF THE HATTAH LAKES

The Hattah Lakes lie within the Mallee country of the western Murray Basin (Fig. 1). To the south the lakes are surrounded by clayey and calcareous east-west oriented longitudinal dunes of the Woorinen Formation (Lawrence 1966) that lie between 52–57 m AHD. To the north and west, and encroaching eastwards across much of the Hattah-Kulkyne National Park, are fine sandy sub-parabolic quartz dune chains of the Lowan-Molineaux Sands (Lawrence 1966) that form the easternmost limit of the Sunset Country dunefield. These dunes lie between 55–77 m AHD, and terminate on the boundary between the topographically lower-lying floodplains of the present

and ancestral River Murray, which still receive periodic flooding. All the lakes lie within sandy sub-parabolic dune country, except for Lake Kramen, which lies on a floodplain terrace.

The sub-parabolic dune country occupied by the lakes is at a lower elevation than the surrounding aeolian plain, often lying 5–10 m below the level of dunes in the Sunset Country several kilometres to the west. Inter-ridge swales are often vegetated by black box, indicating periodic or occasional flooding, and dune crests carry grasses. The lakes, which lie in the lowest points, have broad areas surrounding them that are affected by water and fill during major floods (e.g. 1965 flood; Robinson 1965). Similarly, Chalka Creek often has a well defined but shallow channel surrounded by a broad area of flood-affected country.

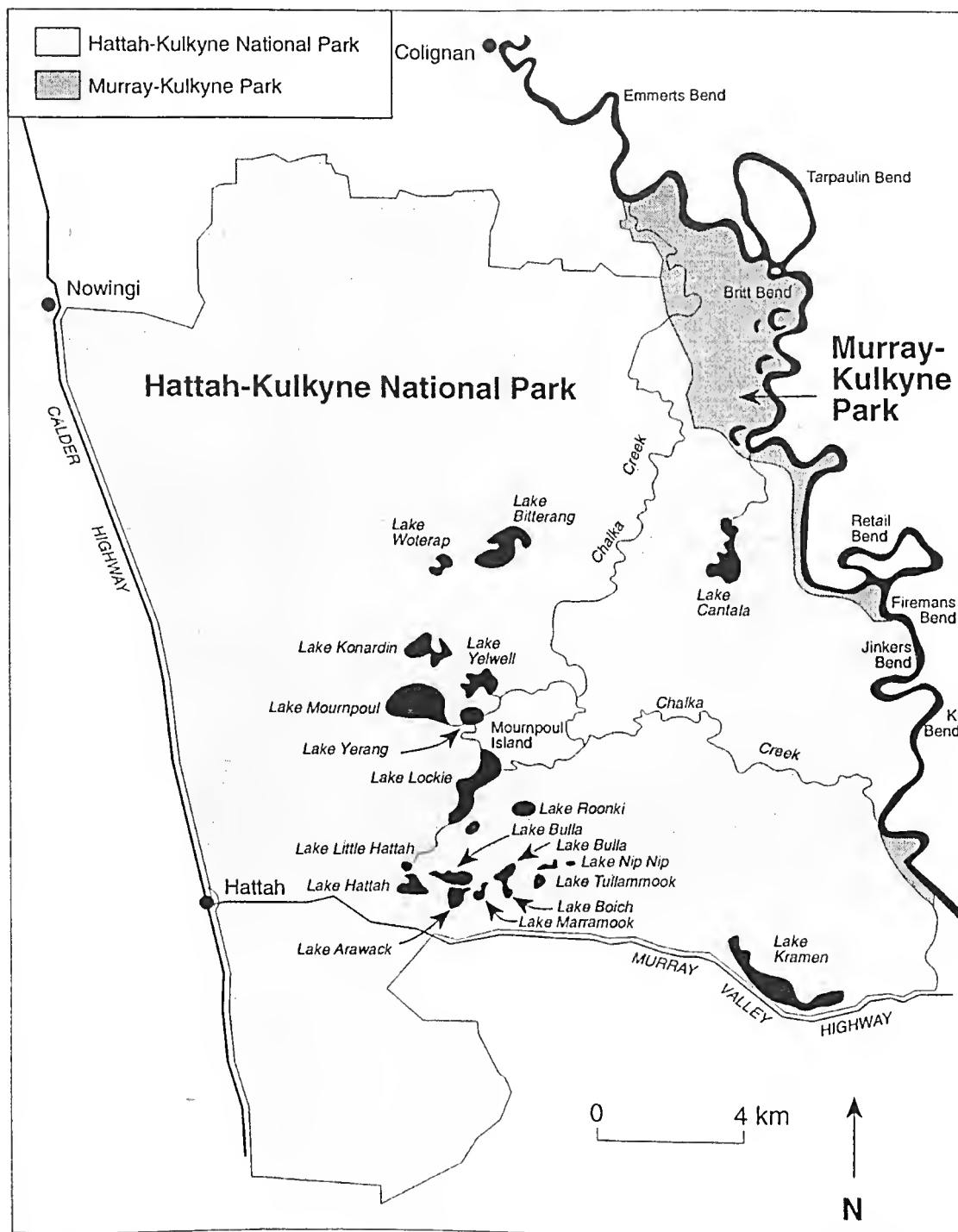
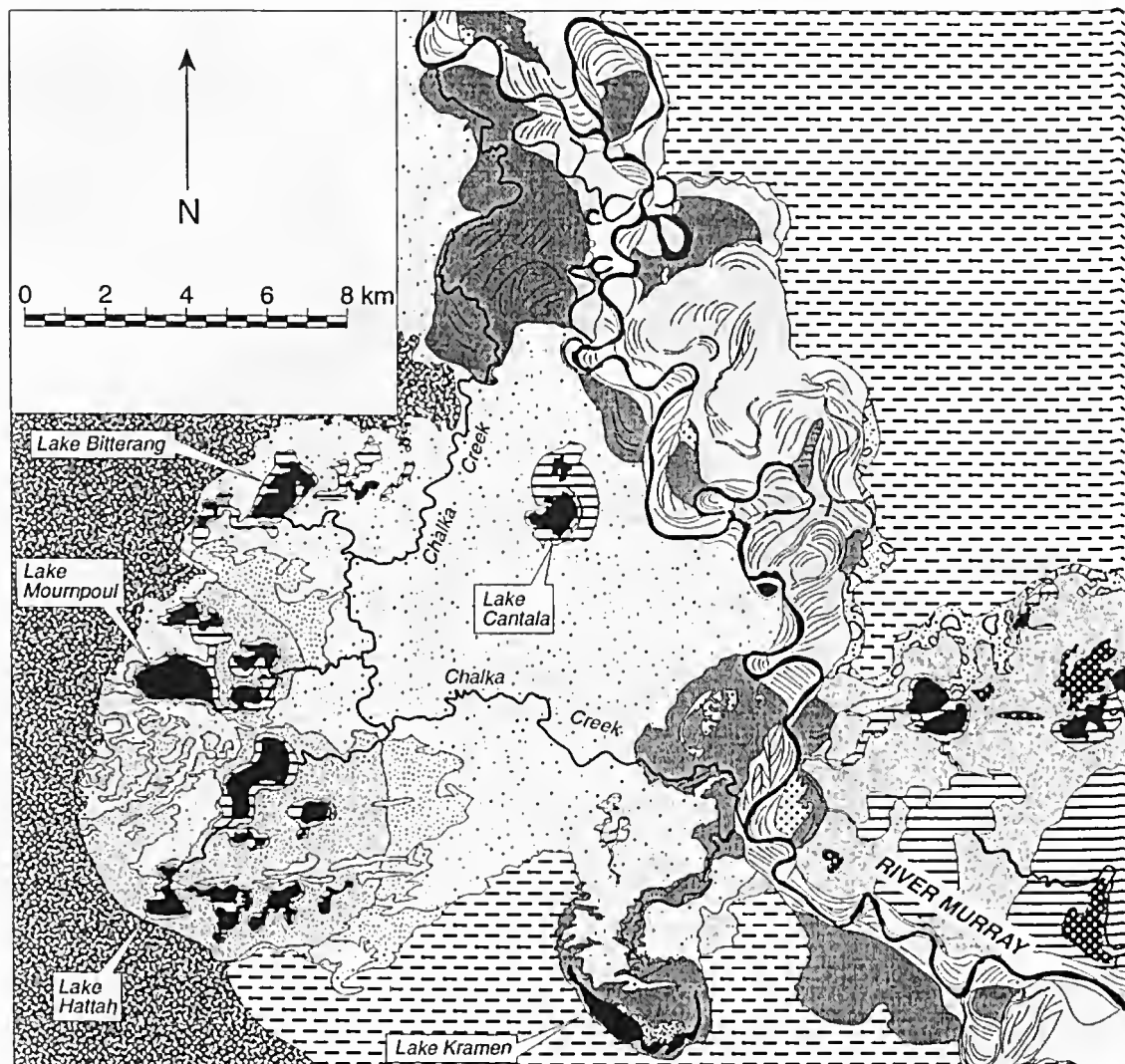


Fig. 2. Hattah-Kulkyne and Murray-Kulkyne National Parks and lakes in northwestern Victoria. Names of features mentioned in text.



Geomorphic Key

Aeolian

- Sub-parabolic dunes: Fine to medium grained quartz sand, weakly calcareous
- Lowan-Molineaux Sands of the Sunset Country
- Clay Lunette: Fine to medium grained gypseous sand and silty clay
- ?Colluvium: eroded mallee dunes
- Hattah Mega-lake: Lunette- calcareous silty sand, well developed red earth soil
- Woorinen Formation: East-west oriented calcareous clayey longitudinal dunes

Lacustrine

- Present lacustrine sedimentation: unconsolidated sand silt and clay
- Hattah Mega-lake: Lacustrine sediments- fine sandy and silty clay, mantled with modern fluvio-lacustrine sediments

Fluvial

- Present Fluvial System: Modern Murray sediments: micaceous point bar sands, clayey and silty meander scrolls
- Present Fluvial System: River Murray floodplain: clay and silt, meander traces, abandoned channels, weak soils
- Low level Floodplain Terrace: Fine sandy source bordering dunes
- Low level Floodplain Terrace: Floodplain sediments: clay and silt, weak meander traces, calcareous soils
- High level fluvial terrace: ?source bordering dunes
- High level fluvial terrace: Floodplain sediments- sand silt and clay, red-brown earth soil

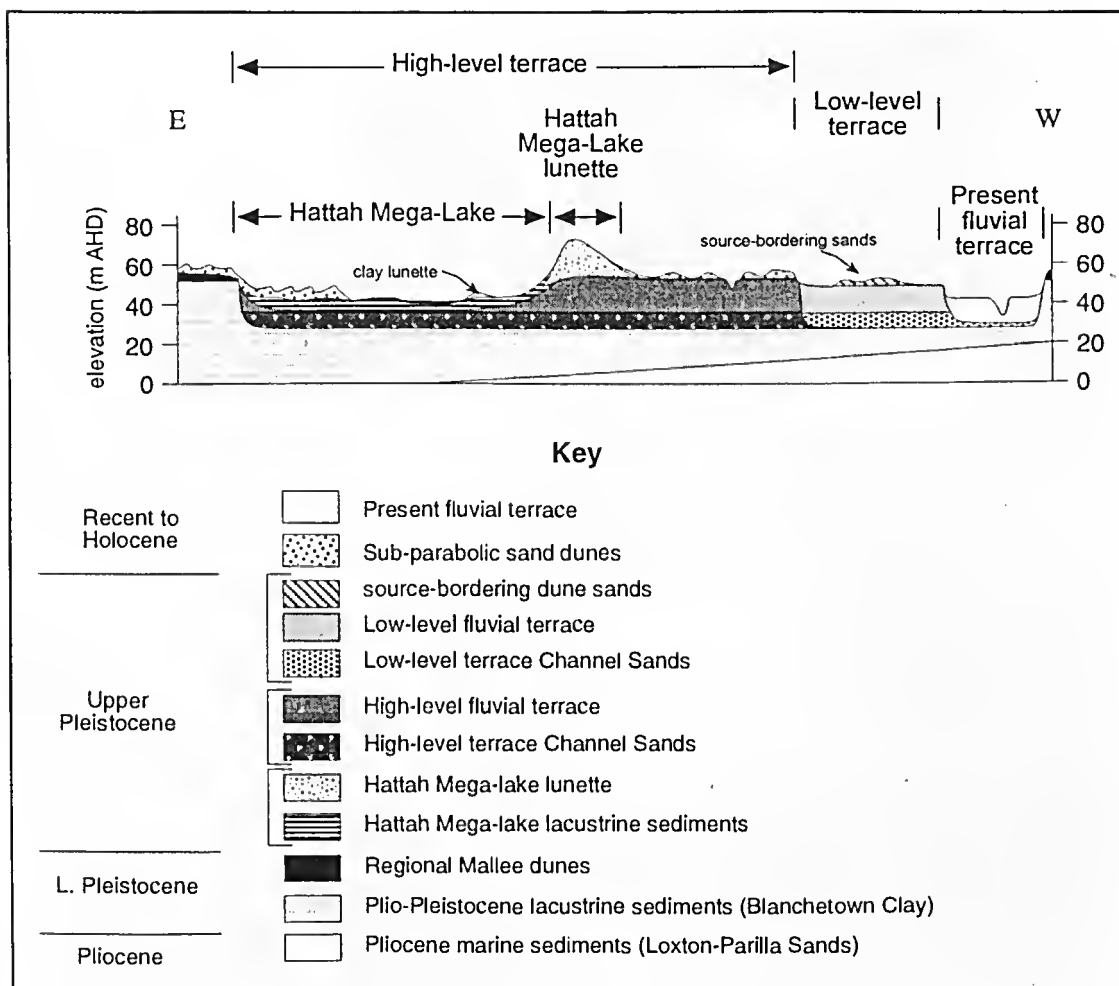


Fig. 4. Simplified east-west cross-section through the Hattah Lakes study area.

LANDFORMS OF THE HATTAH LAKES REGION

The landforms identified within the study area are mapped in Fig. 3. A simplified east-west cross-section of these features is shown in Fig. 4.

Hattah Mega-Lake

The lakes Konardin, Yelwell, Mournpoul, Yerang,

Lockie, Roonki, Hattah, Bulla, Brockie, Arawak, Little Hattah, Marramook, Tullamook, Nip Nip and Boich lie on the floor of a large freshwater palaeo-lake (Fig. 3), that covers an area about 50 km², named the Hattah Mega-Lake (Cameron 1991). To the east the palaeo-lake is defined by a large lunette ridge approximately 10 km long and 1 km wide (Fig. 5), and to the west and south by a change in vegetation, and a subtle topographic drop from 48–56 m AHD to 43 m AHD.

Fig. 3. Geomorphic map of the Hattah Lakes and River Murray in the Hattah-Kulkyne National Park and Murray-Kulkyne Park, north-west Victoria.



Fig. 5. Aerial photograph of the Hattah Mega-Lake, showing limit of palaeo-lake and lunette ridge, and present lakes. Scale: 10 mm = 1 km.

The lunette possesses a broad rounded crest with a maximum elevation of 72 m AHD and gently dipping flanks. It is breached in its centre by the inlet and outlet channels of Chalka Creek which separate the northern and southern ends of the lunette and encircle the subdued, sub-parabolic dunes of Mourmpoul Island. The southern part of the lunette is mantled by sandy dunes. The lunette is composed of well consolidated calcareous fine to medium grained sandy silt and clay, that overlies a shallow clay horizon and calcrete at depth. The lower parts of the lunette are not exposed.

Lacustrine sediments of the Hattah Mega-Lake floor lie between 40–44 m AHD and are mantled by a thin layer of modern-day fluvio-lacustrine sediments. These lacustrine sediments are currently being eroded at the western margins of present lakes, and where exposed, consist of mottled bluish-grey fine sandy and silty clay.

Present lakes and associated features within the Hattah Mega-Lake

The floor of the Hattah Mega-Lake is now occupied by a series of interconnected depressions with the present lakes occupying the topographically lowermost positions just below 40 m AHD and fed by shallow channels connected to Chalka Creek (Fig. 5). The Hattah Mega-Lake floor is vegetated with black box and river red gums that often delineate strandlines, and grow on the margins of lakes, clay pans and channels, whereas grasses predominate on dune sands. All lakes occupy broad shallow basins less than 3 m deep surrounded by thin, gently dipping organic rich, fine grained beach sands overlying dark sandy loams. The eastern sides are often bordered by a lunette.

The lakes within the Hattah Mega-Lake can be subdivided into three groups (Fig. 5): the northern group of the lakes Konardin, Mourmpoul, Yerang and Yelwell; the central group consisting of the lakes Lockie and Roonki; and the southern group consisting of the lakes Little Hattah, Hattah, Bulla, Arawak, Marramook, Brockie, Boich, Tullamook and Nip Nip.

The northernmost group of lakes is separated from the central group by the lobe of sandy dunes to the south and west, and Mourmpoul Island to the southeast (Fig. 5). Flood water enters the lakes through a shallow channel from Lake Lockie, and exits east of Yelwell to the Chalka Creek outlet. The areuate nature of the northwestern edge of Mourmpoul Island and the cliffed inner margin of the northern part of the Hattah Mega-Lake lunette may represent a shoreline of a former larger lake

that may have existed and encompassed these lakes. The dunes of Mourmpoul Island are light brown (but darker than the surrounding parabolic dunes), and quickly pass to a pale orange yellow with depth. They consist of well sorted calcareous fine quartz sand with calcareous aggregates located at about 1 m depth.

The central group of lakes is fed directly from the Chalka Creek inlet and occupy deflated depressions on the floor of the palaeo-lake. The lakes are generally surrounded by dark organic rich sandy loams vegetated with black box and red gums. Of this group of lakes only Lake Lockie has been affected in shape by eastward encroaching dunes.

The southern group of lakes is confined within dune sands that have encroached across the Hattah Mega-Lake floor and onto the lunette ridge to the east (Fig. 5). They are fed by a shallow channel that connects Lake Lockie with Lake Little Hattah, and progressively fill from west to east, with a small breach in the lunette allowing overflow of flood waters to reach Lake Kramen. Except for Lake Little Hattah, the group of lakes is separated from those to the north by a narrow tongue of sandy dunes that trends in an E–W direction. All are strongly influenced in shape by the encroaching dunes, and are separated from one another by poorly organised ridge crests oriented in a N–S direction. The lakes occupy inter-ridge depressions, with the western margin reshaped by the steep lee side of the unstable dunes, and the eastern side reworked by shoreline activity. The persistence of lakes within the inter-ridge depressions, their lobate extension oriented in an E–W direction, and the absence of any permanent lakes just north of the dunes suggests deflation of inter-ridge material.

Smaller lunettes, now vegetated with grasses, bound the eastern side of several existing lakes within, and to the north and east, of the Hattah Mega-Lake. The lunettes are typically 500–600 m in length, 100–150 m in width, and approximately 3 m in height, with an asymmetric cross-section with a steeply dipping inward slope of 6–10° and a gently dipping lee slope between 1–3°. Where the sediments of the lunette are exposed, dark brown loams are characteristic, with moderately sorted fine to medium grained sand and silt-sized clay pellets with occasional Wüstenquartz (silt-sized aeolian quartz dust with a thin coating of argillan of clay and ferric cement; Radezewski 1939) overlain by chernozem soils with fine disseminated carbonate accumulation. At a depth of about 2.4 m secondary precipitates of lenticular gypsum crystals less than 1 mm in size are common.

The crests of the lunettes contain shell middens composed of fragments of freshwater bivalves and occasional shards of animal bone that are probably Aboriginal in origin. The shells, harvested from the lakes, indicate the return of freshwater conditions to the lakes after clay lunette building had ceased.

The dunes that overlie the southern half of the Hattah Mega-Lake lunette are reddish brown throughout. The pigmentation is due to ferri-argillans (see Stace et al. 1968) with irregular thickness, indicating transport of the sediment after eolian development. The absence of similar dunes on the northern section of the lunette indicates that there was no eastward movement of sand across the lake, and may suggest that the north part of the lake may have contained water during this time of dune mobility (Cameron 1991).

The dunes which extend across the lake floor of the Hattah Mega-Lake are preserved as elevated mounds of pale reddish-brown sand that have been reshaped by flood waters. They are pale orange, fine to medium grained, with weakly developed 20 cm thick nodular calcareous horizons often exposed in the base of blowouts at a depth of 4 m. The intensity of pigmentation in these dunes decreases with depth.

Floodplains and terraces of the River Murray

The fluvial sediments of the River Murray and its anabranches form the uppermost sequence of the Late Pliocene to Recent Shepparton Formation (Lawrence 1966) and Late Pleistocene to Holocene Coonambidgal Formation (Butler 1958, 1961). Within the study area, these can be subdivided into three major groups based on morphology, relative topographic position and pedogenesis (Fig. 3; Table 1) (Kotsonis 1991).

High-level floodplain terrace. Topographically high level exposures of fluvial sediments mantled by eastward encroaching sub-parabolic dunes (similar to those described within the Hattah Mega-Lake) occur on the western bank of the River Murray between Jinkers Bend and north-east of Retail Bend (Fig. 2). The elevation of the high level floodplain is similar to the sub-parabolic dune country east of the Hattah Mega-Lake.

Meander scrolls and traces are obscured by dune cover, which masks the westward extent of the floodplain. However, dark heavy clays underlie the dunes and outcrop along the banks of Chalka Creek, and extend toward the eastern margin of the Hattah Mega-Lake. These clays lie on a topographic level similar to exposures along the River Murray, and may represent possible floodplain sediments of the high level terrace. They probably underlie lakes Cantala, Bitterang and Woterap, which require an impermeable base to prevent significant loss of surface water through infiltration. The growth of black box vegetation within inter-dune swales in these areas also suggests water is retained in the near-surface environment even when the surface may be dry.

Exposures along the banks of the River Murray comprise basal ferruginised and cross bedded fine to coarse quartz sandstone, part of the Channel Sands aquifer system (Thorne et al. 1991), overlain by laminated abandoned channel clays and floodplain clays. Individual overbank clay units are thick (>1 m), and typically micaceous. Upper surfaces of channel clays are weathered with red brown mottling, and heavily impregnated with multiple generations of carbonate rhizomes. Solonised brown soils with massive rhizomorph-rich and fine grained nodular carbonate characterise the upper surface of the terrace. The A horizon is absent, probably removed during mobilisation of the overlying dune sands.

	High level terrace	Low level terrace	Present fluvial system
Vegetation	Mallee type	Black box and red gum	Red gum and black box
Meander geometry	Large	Large	Small
Meander wavelength			
Chalka Creek	950–1125 m	300–600 m	175–325 m
River traces	Not visible	2250–2375 m	1225–1800 m
Elevation above present			
Murray River banks	8–10 m	2–4 m	0–2 m
Soil profile	Calcareous solonised brown soils	Calcareous chemozems	Siliceous sands and alluvial soils

Table 1. Summary of the dominant characteristics of the fluvial systems.

Low-level floodplain terrace. Lying 2–4 m below the high level terrace is a low-lying floodplain terrace with a smooth and regular upper surface consisting of dark grey to pale grey-brown cracking clays. Only isolated patches of this terrace remain, onlapping older terraced deposits or the surrounding mallee dune country, or forming elevated benches within lower-lying floodplain sediments of the present river system (Fig. 3). The upper surface is characterised by weak meander traces highlighted by black box vegetation and occasional sandy source bordering dunes.

The boundary between the high level terrace and the low level terrace on the western side of the River Murray is masked by eastward encroaching fine red dune sands. Lake Kramen is located upon dark grey-brown cracking clays of the low level terrace, excavated in a large arcuate abandoned channel in the surrounding Mallee (Fig. 6) and underlain by Channel Sands (Thorne et al. 1991). The area occupied by the lake is mantled by sub-parabolic fine sandy dunes with inter-dune swales reworked by flood waters. The lake lies at the terminus of the depression, and is fed directly from the River Murray, overflow of the Chalka Creek inlet during flooding, and from overflow from the Hattah Mega-Lake. A poorly defined sandy lunette on the eastern side of the lake is probably derived from reworked dune sands.

Source-bordering dunes on the terrace occur on the inner (eastern) side of meanders (Fig. 6). They are typically subdued features that rise 1–2 m above the level of the floodplain, and consist of fine uniform red sand that is significantly paler than the dunes that overlie the high level terrace. These dunes are now vegetated with grasses.

Exposures along banks of the River Murray consist of partly ferruginised and cemented micaceous sandstone, part of the Channel Sands aquifer system (Thorne et al. 1991), overlain by laminated floodplain clays. The sands show well preserved cross bedding and ripple marks with fining upwards sequences. The overlying micaceous laminated floodplain clays are thick (≤ 1 m). Weakly mottled or carbonate rhizomorph-rich upper surfaces occur in many areas, but not as prominently as on the high level terrace. The rhizomorphs occur in irregular columns and can reach lengths of over 30 cm and thicknesses up to 5 cm, with two generations of rhizomorph-rich layers sometimes found in the upper parts of the overbank clays. The upper surface is characterised by a weakly developed calcareous soils (calcareous chernozems) with fine disseminated carbonate in the B horizon.

Present floodplain. The present and active flood-

plain of the River Murray is entrenched and incised within older terraced deposits and occupies the lowest topographic position in the landscape. It is vegetated with river red gum and black box woodland that highlights meander scrolls and abandoned channels. The present floodplain can be subdivided into the sediments of the modern River Murray, and its meander belt (Figs 3, 6). Immature and non-calcareous uniform soil profiles are typical of the floodplain.

The meander belt of the present River Murray lies approximately 1 m below the low level terrace. To the south, it is confined within a narrow belt near the river, but centrally and to the north the floodplain diverges to the east and covers a belt over 4 km wide. The upper surface, typically organic rich with dark friable clays and cracking clays, is slightly undulating with well preserved meander scrolls and abandoned channels. Bank exposures consist of pale red weakly consolidated micaceous quartz sands overlain by weakly laminated mottled pale brown-red sandy clays. Soils are predominantly uniform medium-textured siliceous loams that grade with depth to mottled friable sandy overbank clays.

The modern sediments of the River Murray lie less than a metre below the level of the meander belt and consist of dark brown-red friable and cracking floodplain clays. The upper surface is uneven with well preserved meander scrolls. Micaceous point bar sands are commonly found on the inner margins of meanders. Soils consist of siliceous sands and alluvial soils.

MEANDER, WAVELENGTHS OF TERRACES

Measurements of meander wavelength (sinuosity) derived from traces of river migration on the upper surface of the floodplains can record information concerning palaeo-river flow. Meander wavelength measurements are presented in Table 1.

Meander scrolls are observed on all the terraces except for the high level terrace which is mantled by dunes. However, the distinct change in meander size of the Chalka Creek channel as it traverses the high and low level terraces suggests that it may have developed on an abandoned channel that connected the Hattah Mega-Lake with the river (Fig. 6). Measurements of the meander wavelength of Chalka Creek on the high level terrace vary between 950 to 1125 m, compared to values of 300 to 600 m on the low level terrace. Similarly, the width of the Chalka Creek channel is larger (15 m on the high level terrace compared to 7 m

on the low level terrace). The wavelengths of meander scrolls on the low level terrace are between 2250 to 2375 m.

The meander wavelengths of scrolls and abandoned channels, including oxbow lakes, of the present River Murray and its floodplain are

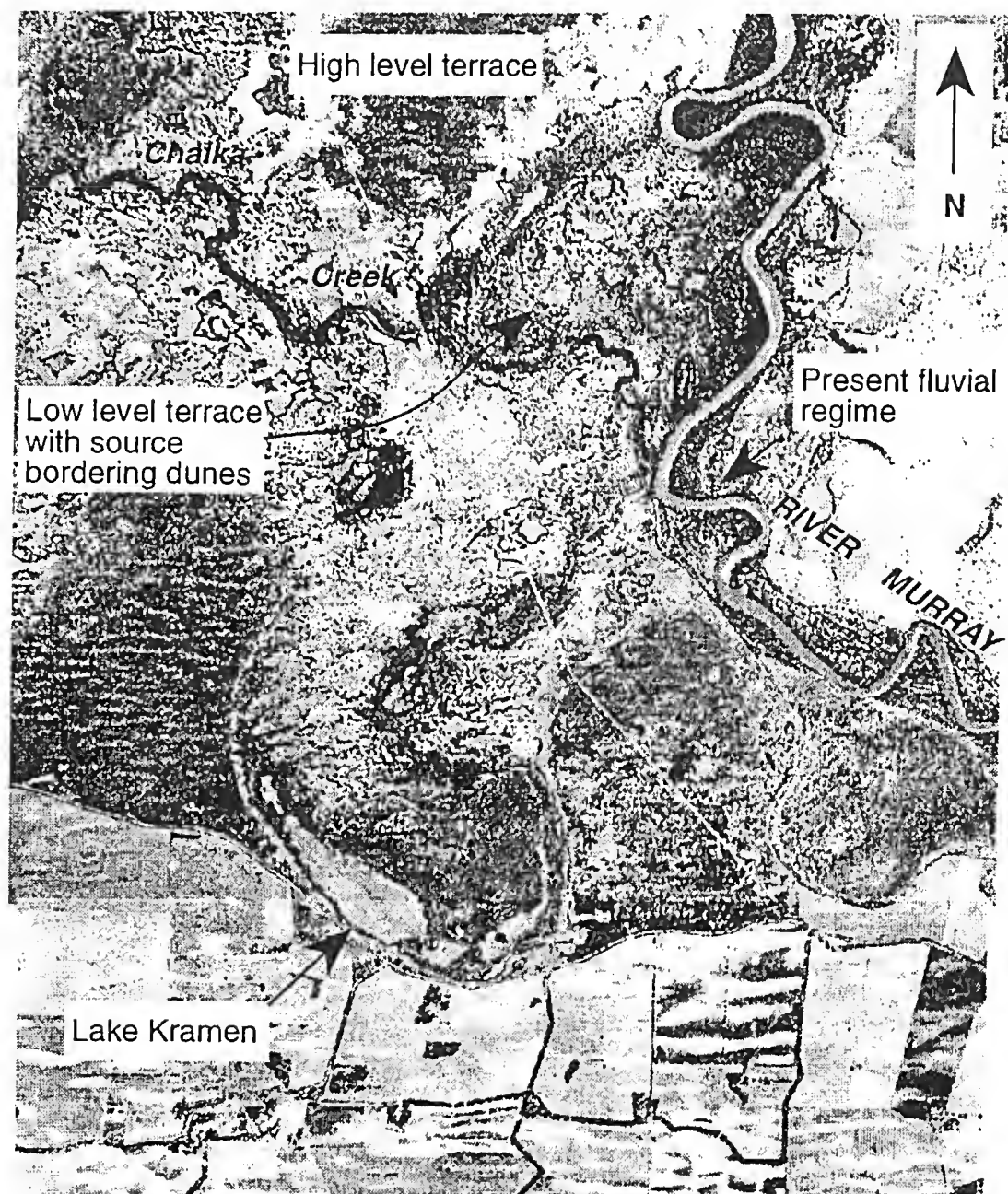


Fig. 6. Aerial photograph of Lake Kramen and Chalka Creek inlet. Note position of Lake Kramen on the abandoned meander of low level terrace, and change in meander geometry of Chalka Creek as it traverses the high level and low level terrace. Scale: 10 mm = 1 km.

smaller as compared to those of the older terraces, with meander wavelengths between 1200 and 1800 m. The larger meander wavelengths of the present system are also observed on Chalka Creek, with younger superimposed meanders between 175 to 325 m in wavelength.

DISCUSSION: GEOMORPHIC SEQUENCE AND CHRONOLOGY

The changes in morphology, pedogenesis and

sediment type permit the construction of a geomorphic and relative chronologic sequence for the Hattah Mega-Lake and the fluvial terraces within the study area. The sequence can be correlated with other Late Quaternary events and landforms across the Murray Basin and southeastern Australia (Stephens 1991; Joyce et al. 1991). Evidence for the fossil nature of landforms is confirmed by the development of soils and the presence of vegetation. The inferred chronology of landform evolution is presented in Table 2.

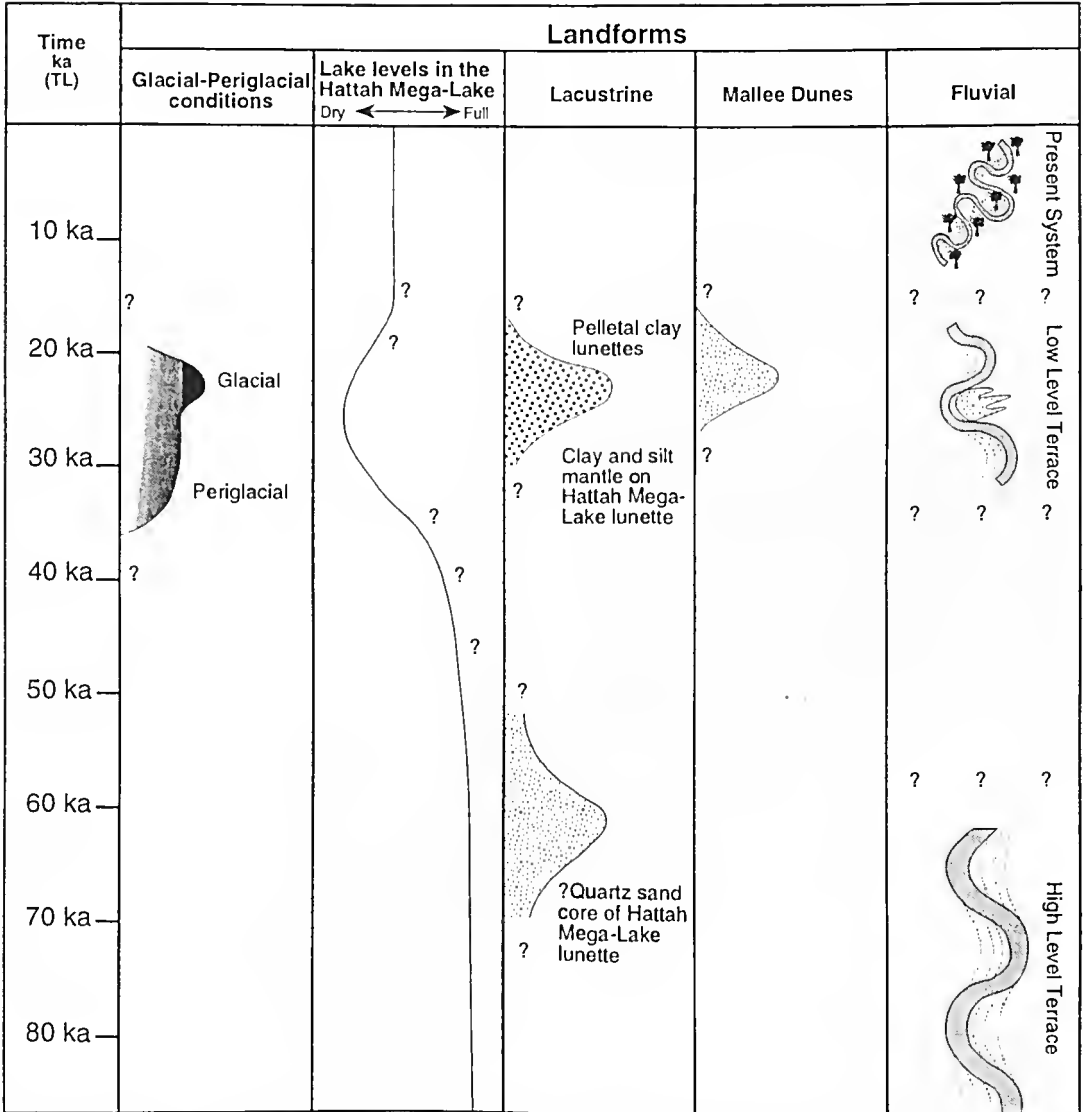


Table 2. Inferred chronology of landform evolution in the Hattah Lakes and River Murray over the last glacial cycle (after Page et al. 1994, 1996; Page & Nanson 1996).

Fluvial systems

The fluvial terraces identified here correspond morphologically to the ancestral river systems described elsewhere for the Murray Basin (Pels 1964a, 1966). The high level terrace is part of the Shepparton Formation (Butler 1958; Lawrence 1966, 1975), and is equivalent to the Rufus Formation of Gill (1973) and Neds Corner Land System of Rowan & Downes (1963), but may be significantly older than the pre-glacial Green Gully/Tallygaroopna sediments at Echuea (Bowler 1978) and Ancestral River I of Pels (1964a) based on the development of well differentiated red earth (duplex) soil profiles with multiple generations of soil carbonate. However, thermoluminescence dating (abbreviated TL) of the Green Gully terrace near Echuea yielded ages between 100 to 65 Ka (Page et al. 1996), and corresponds to the Coleambally phase of fluvial activity on the Riverine Plain (Page and Nanson 1996; Page et al. 1996). This fluvial system may also correspond to the younger Kerarbury or Gum Creek phases, based on pedogenesis and morphology, and TL dated at 55–35 Ka and 35–25 Ka respectively. The high level terrace may be of greater antiquity than that suggested previously by radiocarbon dating.

Traces of original channel morphology preserved as meander scrolls and oxbow lakes on the high level terrace are hidden beneath dune cover. However, meander wavelength and channel size observed along the length of Chalka Creek as it traverses the different terraces (Table 1) suggests that it inherited original channel morphology. The geometry and size of the creek on the high level terrace is significantly larger than the present fluvial regime, suggesting higher river discharge. As a comparison, the channel size of Chalka Creek on the terrace is over three times larger than those observed on the present floodplain.

The low level terrace and the floodplain and sediments of the present River Murray are part of the Coonambidgal Formation (Butler 1958, 1961; Lawrence 1966), as defined by the characteristic grey soils developed on them. Based on the similarity in pedogenesis and morphology, the low level terrace is equivalent to the Coonambidgal II unit of Pels (1964a) and Bowler's (1978) Kotupna Phase fluvial sediments radiocarbon dated at 25 000–30 000 to 15 000 years BP near Echuea. TL dating of the Kotupna channel has yielded similar dates, but slightly older at 34 Ka (Page et al. 1991), and has been correlated to the Yanco Phase of fluvial activity dated at between 20–13 Ka (Page & Nanson 1996; Page et al. 1996).

The sediments of the present River Murray and meander belt form the final episode of fluvial deposition with abandoned channels and point bar traces with dimensions similar to those of the modern Murray. This fluvial system is present along the length of the River Murray and its tributaries, and corresponds to the Goulburn–Murray Phase sediments described at Echuea that developed after about 15 000 years BP (radiocarbon dated; Bowler 1978).

Lakes and lunettes

Hattah Mega-Lake. The entrenchment of the Hattah Mega-Lake below the level of the surrounding Mallee Country on an elevation coincident with the high level terrace indicates that the palaeo-lake developed within the Murray Trench and on fluvial sediments, and is consistent with evidence of possible high level terrace deposits extending towards the eastern margin of the lake. The calcareous soil developed on the Hattah Mega-Lake lunette shows strong pedogenic differentiation with calcrete similar to that described elsewhere in southeastern Australia which dates between 24 000 to 36 000 years BP and older (Bowler 1976; Bowler & Polach 1971; Pels 1964b), suggesting that the palaeo-lake may be of equivalent age. TL dating of the outer lunette of Lake Urana with similar pedogenic differentiation yielded 55–35 Ka (Page et al. 1994). Assuming the Hattah Mega-Lake is of similar TL age to the outer lunette of Lake Urana (55–35 Ka), then the high level terrace must correspond to the Coleambally Phase (100–65 Ka) of fluvial activity and not the younger Kerarbury (55–35 Ka) or Gum Creek phases (35–25 Ka). The large size of the palaeo-lake, combined with evidence of high river discharge on the River Murray, suggests that it contained freshwater.

The Hattah Mega-Lake probably developed on an old meander cut-off on the upper surface of the high level terrace, forming an oxbow lake that was continually fed with flood waters from the River Murray. Continual inflow of water could create a permanent freshwater body from which lakeshore drift could provide sediment for a beach and associated lunette to develop. The lake was probably fed through the wide gap that separates the northern and southern sections of the lunette by the Chalka Creek inlet and outlet channels and now occupied by Mourmpoul Island (Fig. 5), similar to the deltaic channel system and gravel fan of Madowla Park Lagoon that fed Lake Kanyapella at Echuea (Bowler 1978).

Clay lunettes. The weak pedogenic differentiation of the clay rich lunettes combined with their superimposition within the Hattah Mega-Lake indicate that they post-date the development and drying of the palaeo-lake. The presence of salts and gypsum within these lunettes, and the secondary precipitates deeper within the soil profile indicates deposition of these features during conditions of high salinity, which could only be achieved if shallow saline groundwaters, now at 38 m AHD (Thorne et al. 1991) could intercept the landsurface. The conditions required for clay lunette building have been described, where seasonal lowering of saline groundwater tables below the lake floor cause efflorescence of clays and the formation of sand and silt-sized pelletal aggregates that are deflated by prevailing easterly winds (Bowler 1971, 1983; Bowler & Wasson 1984). The exposed upper parts of the Hattah Mega-Lake lunette that comprise silt and clay may record the initial phase of pelletal clay deflation from the lake floor as the lake began to dry.

The presence of Wüstenquartz associated with the pelletal clay indicates widespread aeolian mobilisation synchronous with lunette formation.

Dunes. The similarity in pedogenic differentiation of the various dune forms, with weak calcareous segregations and clay organisation (sandy dunes, dunes of Mournpoul Island, clay lunettes, and soils of the low level terrace with source bordering dunes) suggests regional and contemporaneous aeolian activity. The complete mantle of dunes on the high level terrace, combined with the partial mantle on the Hattah Mega-Lake floor and lunette indicates that dune encroachment proceeded after the drying of the palaeo-lake, and therefore post-dates the terrace. This is supported by the truncation and erosion of the soil developed on the high level terrace by the overlying dunes.

The association of source bordering dunes and the partial encroachment of sandy dunes on the low level terrace (Kotupna Phase; Yanco Phase) suggests aeolian mobility climaxed during deposition of the terrace. Although localised deflation is now occurring in the Mallee as a consequence of European agricultural practices and the clearing of native vegetation, the process of aeolian mobilisation can be described as fossil. However, it is important to note the association between the absence of vegetation and aeolian activity, as widespread dune mobility can be facilitated only by the removal of vegetation, which would expose the landsurface to high velocity winds (Bowler 1978).

The absence of source bordering dunes and the truncation of sandy dunes on older terraces by the present fluvial regime (Goulburn-Murray Phase) indicates that dune mobility had ceased when this fluvial system became active at about 15 000 years BP. Within the Hattah Mega-Lake, the termination of aeolian activity is recorded by the change from saline water in lakes and pelletal clay lunette formation to the return of freshwater conditions as recorded by the harvesting of freshwater fauna from the lakes by the local Aborigines.

THE CLIMATIC SEQUENCE

The landforms of the Hattah Lakes and River Murray floodplains record the history of climatic change that can be quantified here only in relative terms of 'wetter' or 'drier' conditions that encompass the balance between precipitation and evaporation that prevailed regionally across south-eastern Australia. These changes in climate have regional consequences in terms of vegetation and the stability of landforms. Changes in discharge on the River Murray can be related to events at higher altitudes in the southeastern highlands, where glacial and periglacial conditions affected runoff and sediment supply to the Murray Basin plains.

The existence of the Hattah Mega-Lake and lunette, assumed at before 35–55 Ka, indicates a period of significantly higher surface water levels in the Murray Basin, and/or wetter climates with higher precipitation/evaporation ratios than today. High discharge along the River Murray is evidenced by the large meander patterns of Chalka Creek preserved on high level terrace. Assuming water levels in the Hattah Mega-Lake between 45–50 m AHD (water depth between 3–7 m) during this period of lake full conditions, the flood levels on the River Murray required to fill the palaeo-lake need to be several metres above the maximum flows that have been recorded since 1908 (see Bibra & Mason 1967). For example, flood levels 2–7 m above those of the 1964 flood would be required to fill the lake to capacity (the 1964 flood reached only 42.96 AHD), and for comparison, the palaeo-lake would have partially filled during the 1956 flood where water levels in Lake Hattah reached 45.10 m AHD. However, sustaining standing water in the Hattah Mega-Lake under present climatic conditions (present precipitation/evaporation ratio), flood levels of the above magnitude would be required at least once every two years (Bureau of Meteorology Climatic Atlas of Australia 1975).

The Hattah Mega-Lake is assumed to have begun to dry between 35–25 Ka. This period represents the transition between lake-full conditions and high river discharge of the high level terrace, to pelletal clay lunette development and deposition of the low level terrace. Within the Hattah Mega-Lake, this is recorded as segmentation of the palaeo-lake into several smaller lakes, either as a consequence of reduced river flow along the River Murray, or a higher evaporation/precipitation ratio.

Widespread dune activity in the surrounding Mallee Country, within the Hattah Mega-Lake, and on the fluvial terraces began between radiocarbon dates 28 000 to 22 000 years BP (Bowler in Magee & Beaton 1985; Readhead 1988) and TL dates 25–20 Ka (Page et al. 1996) with the appearance of glacial and periglacial conditions in the highlands of southeastern Australia. The loss of vegetation from the plains implies a climatic change which was adverse to the growth of eucalypt and red gum woodland, probably as a result of winters with severe cold and frost, which are detrimental to eucalypt cover (Bowler 1978). The presence of desert-derived dust (Wüstenquartz) indicates climates with intensified seasonality, with hot dry summers producing drought conditions in the continental interior. The loss of woodland vegetation from the floodplains would have facilitated dune growth from exposed point bars during times of low flow. Incidentally, the large meander patterns of the low level terrace (Kotupna Phase sediments) indicate higher river flow than today, probably as a consequence of the reduced vegetation cover and higher runoff in the catchment areas further upstream, along the Murray's anabranches, and in the Southeastern Highlands.

Within the Hattah Mega-Lake, high regional groundwater tables, probably inherited from the past wet phase, combined with the loss of vegetation and increased water infiltration, contributed to the rise in saline groundwaters and salinisation of the palaeo-lake. This process was accelerated by the concentration of salts from drying of the lake under arid conditions (reduced precipitation), resulting in clay efflorescence and the building of pelletal clay lunettes.

The development of the reduced flow and narrow channels of the present fluvial regime (Goulburn–Murray Phase) at about 15 000 years BP marks the cessation of dune building and the return of vegetation to the Mallee plains and the floodplains. This coincides with the disappearance of glacial and periglacial conditions in the southeastern highlands (Bowler et al. 1976) and the return of woodland vegetation to the catchment areas of rivers, resulting in reduced runoff reaching the

Murray Basin plains. This may coincide with the return of freshwater conditions in the Hattah Lakes, which may also extend beyond this time to between 20–13 Ka (Page et al. 1994, 1996). The extension of woodlands is dated at between 13 000 and 10 000 years BP (Raine 1974; Dodson 1974, 1975), and marks the change to climates with higher temperatures and decreased seasonal stresses (Bowler 1978) that promoted the growth of vegetation.

The similarity in morphology between the floodplain system that developed throughout the Holocene (Goulburn–Murray Phase) and the present River Murray suggests moderate climates, comparable to those of today, have persisted since the end of the last glacial cycle. Within the Hattah Mega-Lake pelletal clay deflation ceased as groundwater tables fell below the capillary zone, probably as a consequence of reduced infiltration caused by the return of vegetation to the landscape. The return of permanent vegetation, the growth of eucalypt and mallee scrub in the Mallee and red gum and black box woodland on the floodplains, provided stability to the landscape that prevented significant dune activity during times of severe drought.

SUMMARY AND CONCLUSIONS

The Hattah Lakes within the Hattah–Kulkyne National Park are a group of lakes that developed on the exposed lake floor of a once much larger lake, named the Hattah Mega-Lake. The history of the paleo-lake during the Late Quaternary can be correlated with the record of fluvial sedimentation on the River Murray nearby, and reflects the influence of regional climatic change associated with the last Glacial Cycle. Evidence presented here indicates higher discharge on the River Murray and high lake levels before 35 Ka, when moist conditions prevailed. However, during the Glacial Maximum there was variable river discharge, probably as a consequence of alternating summer drought and higher winter runoff in catchment areas further upstream, and facilitated by the loss of local and regional vegetation. Although discharge during glacial times may have been lower than during pre-glacial times, the loss of vegetation in highland areas and within the study area increased runoff resulting in a greater impact on the landscape. Post-glacial times are characterised by the return of vegetation and landscape stability, with the return of woodland vegetation in catchment areas further upstream significantly reducing runoff to the Murray Basin.

The Hattah Mega-Lake may have formed on an old meander cut-off sometime before the last Glacial Cycle, probably before 35 Ka. The development of the lake and lunette reflects wetter climates than that of today and higher discharge on the River Murray. With the onset of arid conditions associated with the last Glacial Cycle, the Hattah Mega-Lake began to dry, accompanied by the loss of vegetation and widespread dune activation. Numerous smaller deflationary basins developed on the lake floor, and increased salinity caused pelletal clay lunettes to develop. To the east, the River Murray incised within the older terrace and developed a lower lying aggradational floodplain. The disappearance of glacial and periglacial conditions in the highlands heralded the return to more moderate temperatures that promoted the growth of vegetation that stabilised the landscape. The growth of mallee eucalypts on the dunes hindered significant dune mobilisation, whereas the return of river red gums and black box vegetation to the floodplains caused a reduction in bank erosion and the incision of the present river system within older fluvial sediments. Deflation ceased within the Hattah Mega-Lake as falling groundwater promoted the return of woodland vegetation and freshwater conditions within smaller lake basins.

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REFERENCES

- BAKER, B. W. & WRIGHT, G. L., 1978. The Murray Valley; its hydrological regime and the effects of water development on the river. *Proceedings of the Royal Society of Victoria Symposium on the Murray-Darling System* 90(1): 103-110.
- BIBRA, E. E. & MASON, R. G., 1967. *Victorian River Gauging to 1965*. State Rivers and Water Supply Commission, A. C. Brooks, Government Printer, Melbourne, 830 pp.
- BOWLER, J. M., 1971. Pleistocene salinities and climatic change: evidence from lakes and lunettes in southeastern Australia. In *Aboriginal Man and the Environment in Australia*, J. D. Mulvaney & L. Golson, eds, Australian National University Press, Canberra, 47-65.
- BOWLER, J. M., 1973. Clay dunes: their occurrence, formation and environmental significance. *Earth Science Reviews* 9: 315-338.
- BOWLER, J. M., 1976. Recent developments in reconstructing Late Quaternary environments on Australia. In *The Origin of Australians*, R. Kirk & A. G. Thorne, eds, Australian Institute of Aboriginal Studies, Canberra, 55-77.
- BOWLER, J. M., 1978. Quaternary climate and tectonics in the evolution of the Riverine Plain, southeastern Australia. In *Landform Evolution in Australasia*, J. L. Davies & M. A. J. Williams, eds, ANU Press, Canberra, Australia, 70-112.
- BOWLER, J. M., 1980. Quaternary chronology and palaeohydrology in the evolution of the Mallee landscapes. In *Aeolian landscapes in the semi-arid zone of southeastern Australia*, R. R. Storrer & M. E. Stannard, eds, Proceedings of a Symposium held at Mildura, Victoria, Australia, on 17-18 October 1979. Australian Society of Soil Science Inc., Riverine Branch, 17-36.
- BOWLER, J. M., 1983. Lunettes as indices of hydrological change: a review of Australian evidence. *Proceedings of the Royal Society of Victoria* 95(3): 147-148.
- BOWLER, J. M., HOPE, G. S., JENNINGS, J. N., SINGH, G. & WALKER, D., 1976. Geomorphology of the Mallee region in semi-arid northern Victoria and western New South Wales. *Proceedings of the Royal Society of Victoria* 90: 5-26.
- BOWLER, J. M. & POLACH, H. A., 1971. Radiocarbon analyses of soil carbonates: an evaluation of paleosols in southeastern Australia. In *Paleopedology—origin, nature and dating paleosols*, D. Yaalon, ed., International Society of Soil Scientists, Israel University Press, 97-108.
- BOWLER, J. M. & WASSON, R. J., 1984. Glacial age environments of inland Australia. In *Late Cainozoic Palaeoclimates of the Southern Hemisphere*, J. C. Vogel, ed., Balkema, Rotterdam, 183-208.
- BUREAU OF METEOROLOGY, 1975. *Climatic Atlas of Australia*, Australian Government Printer.
- BUTLER, B. E., 1958. Depositional systems of the Riverine Plain of S.E. Australia in relation to soils. *CSIRO, Australia, Soil Science Publication* 10.
- BUTLER, B. E., 1961. Ground surfaces and history of the Riverine Plain. *Australian Journal of Science* 24: 39-40.
- CAMERON, K., 1991. The Geomorphology and Landform Evolution of the Hattah Lakes, Victoria. BSc(Hons) Report, School of Earth Sciences, University of Melbourne, 64 pp, 2 maps (unpublished).
- COLLS, K. & WHITAKER, R., 1990. *The Australian weather-book*. Child & Associates, Frenches Forest, Queensland, 175 pp.

- DODSON, J. R., 1974. Vegetation and climatic history near Lake Keilambete, western Victoria. *Australian Journal of Botany* 22: 709-717.
- DODSON, J. R., 1975. Vegetation history and water fluctuations at Lake Leake, south-eastern South Australia. 11. 50 000 to 10 000 BP. *Australian Journal of Botany* 23: 815-831.
- GILL, E. D., 1973. Geology and geomorphology of the Murray River region between Mildura and Renmark, Australia. *National Museum of Victoria, Memoir* 34: 1-97.
- JOYCE E. B., BOWLER, J. M., STEPHENS, D. I., CAMERON, K. J. & KOTSONIS, A., 1991. Boinkas, lake beds and river terraces of northern Victoria: the Raak Plain and Hattah Lakes-Kulkyne region. *SLEADS Conference 91: Salt Lakes and Arid-zone Environments: Arid zone hydrology, geochemistry, biology, stratigraphy and palaeoenvironments, 9-11 December 1991, Australian National University, Canberra, Abstract* 32-35.
- KOTSONIS, A., 1991. The Geology of the Murray River in the Hattah Lakes Area and Relationships to River Patterns and Soil Development. BSc(Hons) Report, School of Earth Sciences, University of Melbourne, 62 pp, 3 maps (unpublished).
- LAWRENCE, C. R., 1966. Cainozoic stratigraphy and structure of the Mallee region, Victoria. *Proceedings of the Royal Society of Victoria* 79: 517-554.
- LAWRENCE, C. R., 1972. Mildura 1:250 000 geological map. *Mines Department of Victoria, Map* SI/54-11.
- LAWRENCE, C. R., 1975. Geology, hydrodynamics and hydrochemistry of the southern Murray Basin. *Geological Survey of Victoria, Memoir* 30, 359 pp.
- LAWRENCE, C. R. & MACUMBER, P. G., 1974. Balranald and Deniliquin 1:250 000 maps. *Mines Department of Victoria, Map* SI/54-12, SI/54-13.
- MAGEE J. W. & BEATON, J., 1985. Day 1: Willandra Lakes, and Day 2: Raak, Tyrell, Nyah West. *Australian Quaternary Association, Inaugural field meeting, Mildura, 11-13 July 1985, Excursion Notes and Field Guide, parts I and II* (unpublished).
- NORTHCOTE, K. H., 1971. *A factual key for the recognition of Australian soils*. Rellim Publications, South Australia, 123 pp.
- NORTHCOTE, K. H., HUBBLE, G. D., ISBELL, R. F., THOMPSON, C. H. & BETTENAY, E., 1975. *A description of Australian Soils*. CSIRO Publication, Australia, 170 pp.
- PAGE, K. J., NANSON, G. C. & PRICE, D. M., 1991. Thermoluminescence chronology of Late Quaternary deposition on the Riverine Plain of south-eastern Australia. *Australian Geographer* 22(1): 14-23.
- PAGE, K. J., NANSON, G. C. & PRICE, D. M., 1996. Chronology of Murrumbidgee River palaeochannels on the Riverine Plain, southeastern Australia. *Journal of Quaternary Science* 11(4): 311-326.
- PELS, S., 1964a. Quaternary sedimentation by Prior Streams on the Riverine Plain southwest of Griffith, NSW. *Royal Society of New South Wales, Journal and Proceedings* 97: 107-115.
- PELS, S., 1964b. The present and ancestral Murray River System. *Australian Geographic Studies* 2: 111-119.
- PELS, S., 1966. Later Quaternary chronology of the Riverine Plain of southeastern Australia. *Geological Society of Australia, Journal* 13: 28-40.
- RADCZEWSKI, O. E., 1939. Eolian deposits in marine sediments. In *Recent marine sediments, a symposium*, D. T. Parker, ed., American Association of Petroleum Geologists, 496-502.
- RAINE, J. I., 1974. Pollen sedimentation in relation to the Quaternary vegetation history of the Snowy Mountains of New South Wales. PhD Thesis, Australian National University, Canberra (unpublished).
- READHEAD, M. L., 1988. Thermoluminescence dating study of quartz in aeolian sediments from south-eastern Australia. *Quaternary Science Review* 7: 257-264.
- ROBINSON, G., 1965. The Regime of Hattah Lakes. *Proceedings of the Royal Society of Victoria* 79(2): 561-569.
- ROBINSON, G., 1966. Notes on the bankful discharge of a regulated river. *Australian Journal of Science* 28(1): 23-24.
- ROWAN, J. N. & DOWNES, R. G., 1963. A study of the land in northwestern Victoria. *Soil Conservation Authority of Victoria, Publication* TC2, 116 pp.
- SHAW, J. R., 1985. The effects of river regulation and management of water supplies of the Hattah-Kulkyne National Park and the Murray-Kulkyne National Park. Master of Environmental Studies, University of Melbourne (unpublished).
- STACE, T. C., HUBBLE, G. D., BREWER, R., NORTHCOTE, K. H., SLEEMAN, J. R., MULCAHY, M. J. & HALLSWORTH, E. G., 1968. *A Handbook of Australian Soils*. Rellim Technical Publications, Glenside, South Australia, 435 pp.
- STEPHENS, D. I., 1991. The hydrogeology of the Raak depression and its relationship to landform evolution and modern mineral deposition. BSc (Hons) Report, School of Earth Sciences, University of Melbourne, 65 pp, 2 maps (unpublished).
- THORNE, R., HOXLEY, G. & CHAPLIN, I., 1991. Nyah to South Australian Border Hydrogeological Report. *Rural Water Commission of Victoria, Investigations Branch Report* 1988/5, 372 pp.

A SURVEY FOR *SPATHULA TRYSSA* BALL AND OTHER
FRESHWATER FLATWORMS IN THE VICTORIAN ALPS
WITH AN EVALUATION OF THE CONSERVATION STATUS
OF EACH SPECIES

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Eight species of flatworm were identified during a survey of 7 alpine areas in 1993, including 3 species of *Spathula* (Tricladida: Dugesiidae), 4 undescribed species and *Reynoldsonia reynoldsoni* Ball (Tricladida: Dugesiidae). *Spathula tryssa* Ball was relatively common and widespread in two adjacent areas, despite being listed under the *Flora and Fauna Guarantee Act* 1988. Current levels of land use do not appear to be threatening the species with extinction, although cattle grazing may be a localised problem. The IUCN conservation status of the species should be seen as Lower Risk Least Concern. Of the remaining species, two (*S. goubaultae* Ball and an undescribed species) have very restricted distributions on Mt Donna Buang and Mt Stirling respectively, and should be considered to be Vulnerable and Critically Endangered respectively. Three of the species (*S. agelaea* Hall & Ball, *R. reynoldsoni* and a further undescribed species) appear to be either widespread or secure, deserving a Lower Risk Least Concern category, one undescribed species has insufficient data to determine a conservation status (Data Deficient) and the final species (undescribed) requires further taxonomic investigation before conclusions can be drawn.

THE genus *Spathula* (Tricladida: Dugesiidae) consists of nine species restricted to high altitude areas of Australasia (Victoria, New South Wales and New Zealand). All species appear to have a preference for cool, well oxygenated mountain waters (Ball 1977). Of the 6 species of *Spathula* that occur in Victoria, all but one have apparently very restricted distributions, with *S. goubaultae* Ball found only on Mt Donna Buang, *S. truculenta* Ball from Mt McKay (but also from Mt Kosciuszko), *S. foeni* Ball from a single site at Buxton and *S. camara* Ball from Falls Creek. The remaining species, *S. tryssa* Ball, has only been found at two spring localities on Mt Buller (Ball 1977; Hay & Ball 1979). One record near Mt Howitt (Powling & Sedgley 1984) was identified only as *Spathula* cf. *tryssa*, but was made without sectioning and the specimen has been lost (D. Hay, pers. comm.). The final species, *S. agelaea* Hay & Ball, appears to be more widespread, found on Mt Buffalo and the Falls Creek-Mt Hotham area (Hay & Ball 1979).

S. tryssa is a medium size flatworm (around 8 mm in length) and differs from most other species of the genus by the lack of pigment (a characteristic shared only with *S. goubaultae*), giving it a white appearance in the field and the lack of eyes (shared only in Victoria with the pigmented *S. camara*). These characteristics do not allow formal identification in the field, but external characters can be used to identify specimens in the laboratory. Formal identification of *Spathula* species is only possible by serial sectioning of properly preserved specimens.

On the basis of the limited distribution and perceived threats from alpine resort development and grazing, *S. tryssa* was listed under Schedule 2 of the *Flora and Fauna Guarantee Act* 1988. In 1993, a comprehensive survey for *S. tryssa* was conducted to better determine the distribution and conservation status of the species and to collect information on the preferred habitat and ecology of *S. tryssa* and other flatworm species that may occur with it. This paper presents the results of that survey.

SURVEY METHODS

Seventy survey sites for freshwater flatworms were identified from maps and local knowledge (a list of sites is available from the senior author). Sites were concentrated in 7 main areas: Mt Buller–Mt Stirling; Mt Hotham; Mt Howitt; Mt Buffalo; Lake Mountain; Mt Donna Buang; and Mt Baw Baw (Fig. 1). Sampling sites were more concentrated in the Mt Buller–Mt Stirling area, the major area where *S. tryssa* was known to occur.

Sites were sampled in December 1993. Emphasis was placed on collecting white unpigmented species to maximise the inclusion of *S. tryssa*. Emphasis was also placed on springs as this was the habitat of previously collected specimens (Hay & Ball 1979; Powling & Sedgley 1984), however other habitats were also searched to see if they were utilised. At each site, rocks and other in-stream habitat were searched by eye. Rocks were removed from the stream and the underside also searched. Specimens of flatworms remaining on hard sub-

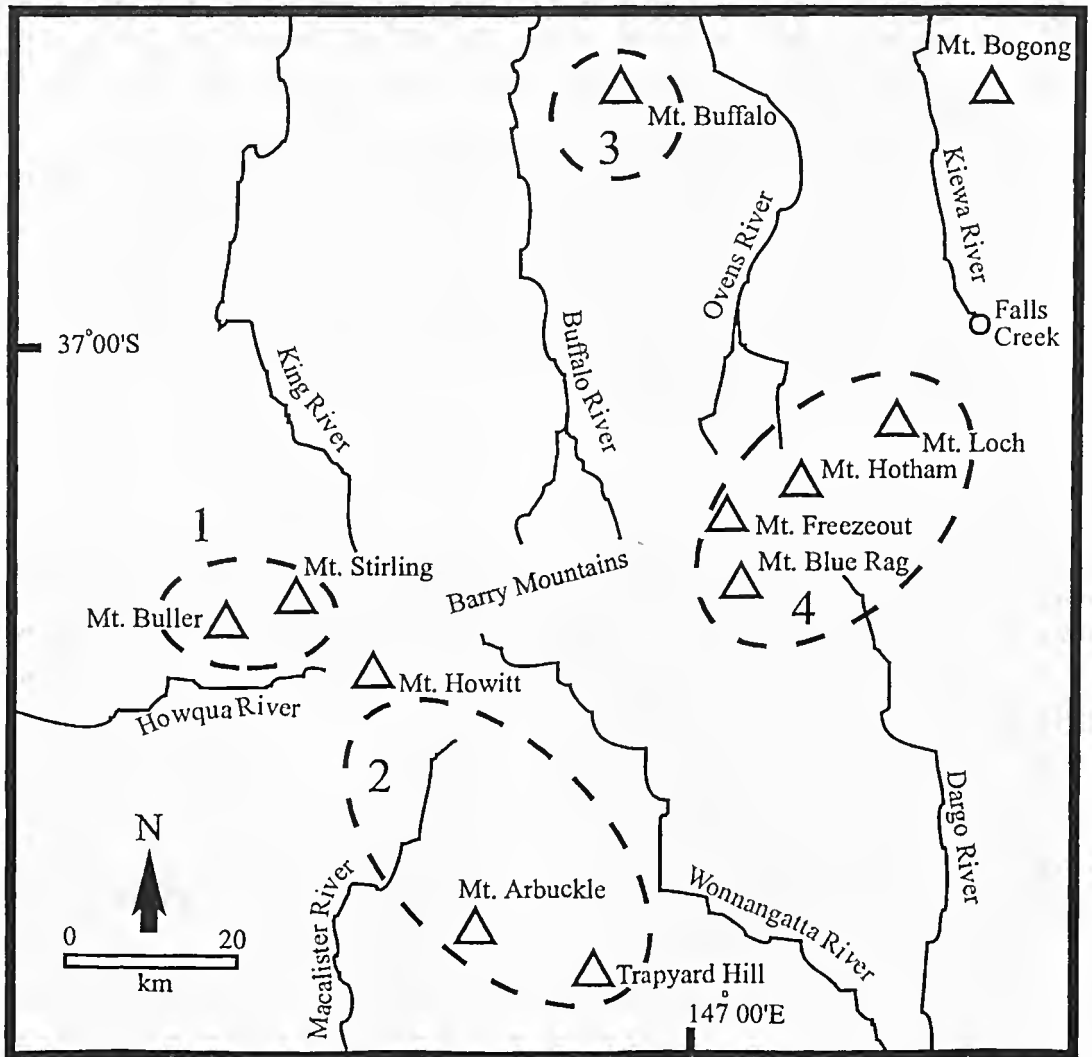


Fig. 1. Map of the central alps of Victoria showing the location of the 4 main sampling areas. More isolated areas to the south west (Mt Baw Baw, Mt Donna Buang and Lake Mountain) are not shown.

strate after removal from the water were covered by fixative solution, so they relaxed in a relatively flat position, and then sluiced off or removed using a fine brush. Animals on soft substrate were collected by brush or fine pipette and placed straight into fixative. As it is not possible to identify species in the field, specimens were killed in Dawar's solution (Dawar 1973) as this preserves much of the external morphology very well, as well as providing good fixation of internal anatomy for sectioning. Specimens were kept in Dawar's solution for about 24 hours before being transferred to alcohol.

IDENTIFICATION OF SPECIMENS

All specimens collected were identified using external morphology. Features used were color, presence or absence of eyes and number and position of sensory pits and fossae. These were sometimes comparatively subtle characters but could be seen with care. Some of these characters have previously been considered to be only apparent in sectioned specimens (eg. Ball 1977) but the use of Dawar's solution enabled these characters to be seen, greatly improving the identification of specimens.

The identification of selected specimens was confirmed by sectioned material. Twenty-one specimens of *S. tryssa*, 7 specimens of Species 1 and 1 specimen each of *S. goubaultae*, *S. agelaea* and Species 2 were sectioned. Whole specimens were preserved in alcohol and were lodged with a few specimens on slides in the Museum of Victoria, Melbourne.

RESULTS

Species found during this study

Eight species of flatworm were collected and identified from 58 of the 70 sites surveyed (Table 1). This included three species of *Spathula* (*S. tryssa*, *S. goubaultae* and *S. agelaea*). Another unpigmented dugesiid species *Reynoldsonia reynoldsoni* Ball was also identified, and significantly, four previously undescribed species (designated Species 1–4; Table 2) were located. Although some of the undescribed species appear to be similar to existing *Spathula* species, we have not ascribed a generic designation to them. Another large white flatworm belonging to a different order (Alloeocoella, family Prorhynchidae) was also found, but is not discussed in detail here.

Distribution of flatworm species

Spathula tryssa

S. tryssa was found at 17 of the 26 sites sampled around the Mt Buller–Mt Stirling area and at 7 of the 10 sites in the adjacent Howitt–Wellington massif (areas 1 and 2 in Fig. 1). On both these highland areas, the species could be found relatively easily in small spring-fed water bodies above 1475 m, often in high abundances. Examination of sectioned specimens from this study indicated that specimens in both these alpine areas were the same species. The two known localities on Mt Buller recorded in the literature could not be identified exactly, due to the large number of sites where the flatworms were present and the relatively vague nature of the original site descriptions (eg. the type

Collection area	Number of sites	<i>try</i>	<i>age</i>	<i>gou</i>	<i>Rey</i>	1	2	3	4
Mt Buller	17	12	0	0	0	0	0	0	0
Mt Stirling	5	3	0	0	0	2	0	0	0
Corn Hill	4	2	0	0	0	0	0	0	0
Howitt–Wellington area	10	7	0	0	0	0	0	2	0
Mt Baw Baw	1	0	0	0	0	0	0	0	1
Mt Donna Buang	1	0	0	1	0	0	0	0	0
Mt Hotham–Dinner Plain	15	0	1	0	0	0	4	3	9
Dargo High Plains	10	0	1	0	0	0	5	4	1
Mt Buffalo	5	0	1	0	5	0	0	0	0
Lake Mountain	1	0	0	0	0	0	0	0	1
Mt Skene	1	0	0	0	0	0	0	0	0
Total	70	24	3	1	5	2	9	9	11

Table 1. Distribution of flatworms collected during this study. *try* = *S. tryssa*, *age* = *S. agelaea*, *gou* = *S. goubaultae*, *Rey* = *R. reynoldsoni*, 1 = Species 1, 2 = Species 2, 3 = Species 3, 4 = Species 4.

locality is described by Ball (1977) as 'Headwaters of Chalet Creek at 4600 ft on Mt Buller'. No specimens of *S. tryssa* were identified from the 34 sites sampled in other alpine areas, suggesting that the species is restricted to these two contiguous areas.

Spathula agelaea

S. agelaea was present at 3 sites, widely spread on Mt Buffalo, Mt Hotham-Dinner Plain and Dargo High Plains (areas 3 and 4 in Fig. 1), confirming the distribution noted by Hay & Ball (1979). This species was described by Hay & Ball (1979) from asexual specimens as they were unable to find any that were sexually mature. One sectioned specimen of *S. agelaea* was sexually mature and confirmed its specific uniqueness. At the time they suggested the species may be an asexual race of *S. tryssa*, but the sectioned specimen was clearly not *S. tryssa*.

Spathula gorbaultae

S. gorbaultae was confined to Mt Donna Buang, found only at the one locality sampled on that mountain.

Reynoldsonia reynoldsoni

R. reynoldsoni was found only from 5 sites, all on Mt Buffalo (area 3 in Fig. 1).

Species 1

The undescribed Species 1 was found only at two adjacent springs about 50 m apart on Mt Stirling (area 1 in Fig. 1). At one site it was found with

S. tryssa. As it was not recorded at any of the other 26 sites in the Mt Buller-Mt Stirling area, it would appear to be the species with the most restricted distribution found in this study.

Species 2

Species 2 was moderately common around Mt Hotham-Dinner Plain and the Dargo High Plains (area 4 in Fig. 1), being found at 9 of the 25 sites with records spread over the entire sampling area.

Species 3

Species 3 occurred at 9 of the 35 sampling sites in both the Mt Howitt and Mt Hotham area (areas 2 and 4 in Fig. 1).

Species 4

Species 4 was found at 11 widespread sites, most commonly in the Mt Hotham-Dinner Plains area, but also on the Baw Baw Plateau, Dargo High Plains and Lake Mountain. As this species is probably a complex of species, taxonomic problems need to be resolved before distributional data can be further examined.

DISCUSSION

Distribution, species associations, habitat and ecology of Spathula tryssa

The data collected here suggest that *S. tryssa* is far more widespread than originally thought. While previously only recorded from the streams near the

Species	Description
Species 1	A pigmented species with an unpigmented ventral surface, and possessing obvious eyes. This species is very similar to <i>Spathula camara</i> in internal anatomy and sectioning of more specimens is required to differentiate the two. However, the presence of eyes distinguished it from all the pigmented species, including <i>S. camara</i> .
Species 2	An unpigmented species similar to <i>S. tryssa</i> but differing from it in, among other things, possessing only one pair of sensory pits and testes confined to the pre-pharyngeal region (<i>S. tryssa</i> has 3 pairs of pits and testes situated through the body length).
Species 3	A pigmented species. The combination of pigment, 2 pairs of ciliated pits, 1 pair of sensory fossae and no eyes suggest it to be a distinct, yet undescribed species.
Species 4	A pigmented species with a paler undersurface, varying from very pale to very dark grey. The variability in color suggest this designation may include more than one species, including <i>S. camara</i> .

Table 2. Description of undescribed Species 1-4 found during the study.

summit of Mt Buller, the species is now known to exist over a large area of the Howitt-Wellington massif (area 2 in Fig. 1). It also suggests that the lost specimen identified as *Spathula* cf. *tryssa* (Powling & Sedgley 1984) may well have been of that species (although due to the discovery of several undescribed species in this survey, this cannot be confirmed).

S. tryssa was found predominantly in spring-fed waters. Where these waters emerge from the ground, they are very cool and very shallow, often no more than a damp seep. The flatworms were easiest to collect in the alpine herbfield and in forest where the spring or seep had collected into pools or runnels, either naturally or in roadside gutters. *S. tryssa* was also found, but generally in low or moderate numbers, in creeks although they had possibly washed in from the spring-fed habitats further upstream. No specimens of *S. tryssa* were found in spring or creek habitats below about 1470 m, despite the apparent similarity of many of the lower altitude sites.

S. tryssa was usually the only flatworm species in the spring, but on occasions occurred with the prorynchid and at one locality with Species 1 and two localities with Species 3. With both Species 1 and Species 3, individuals of the two species were found clumped together under a single rock.

The species was abundant at several of the localities listed. At the site where it was most abundant, Macalister Springs, hundreds of individuals were found under one rock and flatworms were found under many rocks, as well as wandering on the substrate and water surface. The total population at this site was extremely large. The specimens were also much larger at this site, approximately twice the size of individuals at any other site.

The conclusion by Hay & Ball (1979) that the species retreats into the groundwater to escape drying of the surface water would appear to be valid. Most water bodies where specimens were collected would clearly dry up in most years, maybe several times, and flatworms are unable to withstand desiccation. Drying of potential habitat reduced the number of areas that could be sampled during this study on the south side of Mt Buller, Mt Stirling and parts of the Howitt High Plains area. Use of the groundwater would also explain the widespread occurrence of the species in the Buller-Corn Hill-Stirling area as flatworms could easily move into all available water bodies in the groundwater. Movement between such small, short-lived water bodies would otherwise be very difficult for a freshwater flatworm.

Hay & Ball (1979) state *S. tryssa* never experiences temperatures greater than 9°C and their laboratory study found viability of the species at 10°C to be very low. This lead them to suggest that *S. tryssa* retreated into the groundwater to avoid drying and high temperatures. During the current study specimens were found in higher temperatures, up to 19°C, although these high temperature habitats may have been areas that were about to dry out and had been disconnected from the groundwater, stranding the flatworms. As such, the temperature may not be representative of the habitat of successful flatworms.

The restriction to altitudes over 1470 m, if influencing distribution below ground as well as above ground, means that the population in the Mt Howitt-Mt Wellington area has been genetically distinct from the Mt Buller area populations for at least 15 thousand years and possibly up to 20 million years. Even within each of the two broad areas it is possible that populations are isolated and unable to interbreed, so that the population on Mt Stirling may now be genetically distinct from those of Corn Hill and Mt Buller. Populations in the Mt Howitt area may be even more disjointed.

Surface waters were often degraded after leaving the spring by collecting in roadside gutters, on ski runs or due to grazing by cattle. While found in roadside gutters and on ski runs, the flatworms were rarely found in areas where grazing had occurred. On Mt Stirling, no flatworms were found in the most trampled spring seep area. Both species of flatworms on Mt Stirling were found in areas that were amongst slightly higher vegetation which may suggest they need cover for protection or cooling. Grazing and wandering horses may reduce this cover and may be responsible for the absence of the flatworms in the trampled area but the evidence is not conclusive. In the Mt Howitt area, the absence of flatworms from trampled springs may also indicate a loss of habitat due to grazing.

Conservation status of Spathula tryssa

S. tryssa is restricted to two main adjacent areas of alpine Victoria. Taxonomic work suggests it is the same species in both main areas although only a few specimens have been sectioned in this and previous studies.

Based on the IUCN categories (IUCN 1994), there are no quantitative measures of population reduction, abundance or probability of extinction for *S. tryssa*, but the extent of occurrence is relatively large (perhaps extending over 2000 km²).

Hence the category of Critically Endangered is not appropriate, but Endangered (extent of occurrence less than 5000 km²) or Vulnerable (less than 20000 km²) may be appropriate.

The movement of the species through the groundwater means that the number of populations or subpopulations cannot be estimated, but is likely to be large. While local extinction seems to have occurred in several individual sites, possibly due to grazing, this cannot be seen as the same as extinction of a location or population as only part of the groundwater pool would have been disturbed and recolonisation of disturbed habitats would be expected to be relatively easy. Hence while the quality of the habitat is degraded at several points, there is no evidence for a decline in the area of occupancy, a key requirement for the designation of a conservation status.

In conclusion, *S. tryssa* is common and widespread on two mountain massifs, although probably as distinct populations. Several populations occur within the Alpine National Park although they may be locally adversely affected by grazing within the park. *S. tryssa* is apparently unaffected by other current land use practices. The greatest threats locally are damage to areas where the groundwater reaches the surface and over a larger scale, alteration to the groundwater quality and quantity. It seems that currently the species is not threatened with extinction and should be placed in the Lower Risk Least Concern category. As a result of the data collected during this survey, the species has been delisted under the *Flora and Fauna Guarantee Act 1988*.

Conservation status of other species

Spathula gorbaultae

This species is confined to Mt Donna Buang. Although listed as common by Hay & Ball (1979), specimens were found at only one locality during this study. This may be due to the absence of groundwater at the time or may indicate reduction in numbers of this species. However, with a similar distribution and habitat to the Mt Donna Buang wingless stonefly *Riekoperla darlingtoni*, restricted to small upland streams on Mt Donna Buang, this species should be similarly classified as Vulnerable under IUCN (1994) Criterion D2 with a population

characterised by an acute restriction in its area of occupancy (typically less than 100 km²) or in the number of locations (typically less than 5). Such a taxon would

thus be prone to the effects of human activities (or stochastic events whose impact is increased by human activities) within a short period of time in an unforeseeable future, and is thus capable of becoming Critically Endangered or even extinct in a very short period. (IUCN 1994: 20)

The taxon would thus be suitable for listing under the Flora and Fauna Guarantee Act 1988.

Spathula agelaea

This species appears to be present at widespread localities on Mt Buffalo in the National Park and Mt Hotham–Mt Bogong area in ski resort areas, National Park and private grazing areas. It appears to be as widespread as *S. tryssa* and deserves the same IUCN conservation status (Lower Risk Least Concern).

Reynoldsonia reynoldsoni

Although only located on Mt Buffalo, this species is widespread over the plateau and should be considered as secure (Lower Risk Least Concern).

Species 1

Species 1 is the species with the most restricted distribution found in this study. Only found at two sites (probably representing a single connected population), it is clearly under threat from extinction, particularly if horse riding, grazing or other disturbance affects the known habitats. This species should be classified as Critically Endangered under the IUCN categories, and would be suitable for listing under the *Flora and Fauna Guarantee Act 1988*.

Species 2

The distribution of Species 2, while found in a relatively small area around Mt Hotham, cannot be determined as it was spread over the entire sampling area. It is possible that the range extends some considerable distance further east or north. Without adequate data on the range of the species, it should be considered as Data Deficient, defined by the IUCN as a species where 'there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status' (IUCN 1994: 14). As the species is present at a number of sites within the Alpine National Park, the impact of grazing is likely to be similar to that on *S. tryssa*.

Species 3

Species 3 was found in two well separated discrete areas, so may be seen as widespread. It appears to be as widespread as *S. tryssa* and deserves the same IUCN conservation status (Lower Risk Least Concern).

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REFERENCES

- BALL, I. R., 1977. A Monograph of the genus *Spathula* (Platyhelminthes : Turbellaria : Tricladida). *Australian Journal of Zoology, Supplementary Series No. 47*, 43 pp.
- DAWAR, B. L., 1973. A combined relaxing agent and fixative for triclads (Planarians). *Stain Technology* 48: 93-94.
- HAY, D. A. & BALL, I. R., 1979. Contributions to the biology of freshwater planarians (Turbellaria) from the Victorian alps, Australia. *Hydrobiologia* 68: 137-164.
- IUCN, 1994. *Red List Categories*. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- POWLING, J. & SEDGELY, M. G., 1984. Mistaken identity of a worm at Macalister Springs, Victoria. *Victorian Naturalist* 101: 191-192.

AUSTRALIAN TERTIARY APATOPYGIDAE (ECHINOIDEA)

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The age, stratigraphic horizon and distribution of the three known Australian apatopygids and their associated echinoid faunas are discussed. *Apatopygus vincentinus* (Tate 1891) is redescribed and restricted to the Middle–Late Eocene (Johannian–Aldingan, Bartonian–Priabonian). Two new taxa are documented: *Apatopygus mannumensis* sp. nov. from the Late Oligocene–Middle Miocene (Janjukian–early Bairnsdalian, Chattian–Serravallian) and *Porterpygus devlinensis* sp. nov. from the Early Miocene (Longfordian, Aquitanian–Burdigalian). The latter is the first fossil record of the genus.

The relationship between extant and fossil species of the family in Australia and New Zealand is reviewed, taking into account the Late Paleocene–Early Eocene occurrence of *Apatopygus* in the Chatham Islands, New Zealand.

Key words: Echinoidea, Apatopygidae, Tertiary, Australia, new taxa.

ALTHOUGH much has been written about the extant New Zealand type species of *Apatopygus* Hawkins 1920 (*Nucleolites recens* Milne Edwards 1836) and the extant Australian *A. occidentalis* Clark 1938, the fossil record of this genus from the Tertiary of Southern Australia has been virtually ignored.

Tate (1891) briefly described the cassiduloid *Echinobrissus vincentinus* from the Late Eocene of Aldinga, South Australia, but the species, referred to *Apatopygus* by Philip (1970), was not mentioned in the major systematic works of Hawkins (1920), Lambert & Thiéry (1924, 1925), Brighton (1929), Mortensen (1948), Kier (1962, 1966) and Baker (1983). However, reference to Tate's species, under the original binomen, appear in several 19th and 20th Century faunal lists. Clark (1946) speculated on its possible relationship to the genus *Apatopygus*, but assigned it to *Nucleolites*.

Echinobrissus vincentinus has, in the past, included specimens from the Middle–Late Eocene and from the Late Oligocene–Middle Miocene. The first record (that can be verified by recent collecting) of the Late Oligocene–Middle Miocene form, here described as *Apatopygus mannumensis* sp. nov., is from Spring Creek, Torquay, Victoria (Hall & Pritchard 1896). Ludbrook (1961) first recorded its presence in the Murray River cliffs, listing 'cf. *Echinobrissus vincentinus* Tate' as occurring in the upper Mannum Formation at the Mannum Pumping Station, South Australia. However, it is only in the last few years that sufficient Late Oligocene–Middle Miocene specimens have become available, following extensive

collecting in South Australia and Victoria by R. J. and F. Foster, F. C. and E. Holmes, and C. AhYee and J. Krause, to allow a detailed comparison with the Middle–Late Eocene *Apatopygus vincentinus*.

Porterpygus devlinensis sp. nov., the first fossil record of *Porterpygus* Baker 1983, is also based on specimens collected by R. J. and F. Foster.

AGE, STRATIGRAPHY AND DISTRIBUTION

Middle–Late Eocene localities

Apatopygus vincentinus occurs in five Middle–Late Eocene formations in southern Australia; the Tortachilla Limestone at Maslin Bay, the lower unit of the Kingscote Limestone on Kangaroo Island and the Muloowurtie Formation on Yorke Peninsula, in the St Vincent Basin, South Australia (Fig. 1, localities 1–3); and the Wilson Bluff and Toolinna Limestones at Toolinna Cove in the Eucla Basin, Western Australia (Fig. 1, locality 4).

1. The Tortachilla Limestone, considered the origin of Tate's syntypes from 'Aldinga', crops out in the cliffs at the southern end of Maslin Bay, north of Blanche Point, about 40 km south of Adelaide. It comprises a basal bryozoal ferruginous sand, up to 1 m thick, grading up into 1 m of richly fossiliferous limestone, which is overlain irregularly by 1 m of glauconitic fossiliferous limestone (Lindsay & Alley 1995). The formation contains a rich echinoid fauna (Appendix 1) dominated by cassiduloids.

2. The lowest unit of the Kingscote Limestone exposed in coastal cliffs at Kingseote, Kangaroo Island, is a coarse grained, yellow-buff bioclastic limestone which correlates in part with the Tortachilla Limestone (Lindsay & Alley 1995). Generally this unit, particularly at the southwestern end of the cliffs towards Brownlow Beach, contains a similar echinoid fauna to that of the Tortachilla Limestone, although there are often minor diagnostic and size differences between mainland and island specimens of the same species.

3. The Muloowurtie Formation, which also correlates in part with the Tortachilla Limestone (Lindsay & Alley 1995), crops out in the vicinity of Harts Mine and Muloowurtie Point, on the east coast of Yorke Peninsula, south of Ardrossan. Consisting primarily of yellow calcareous clays and varicolored sands it disconformably overlies the Lower Cambrian Kulpura Limestone (Stuart 1970).

4. Philip (1970) identified *Apatopygus vincentinus* at Toolinna Cove, approximately 380 km southeast of Eucla. The specimens occur 9–25 m above sea level in the white chalky bryozoal calcarenite of the upper part of the Wilson Bluff Limestone and

in the overlying coarse grained bryozoal calcarenite of the Toolinna Limestone.

Age determination. The Tortachilla Limestone, the most time restricted of the five formations, has in the past been considered early Late Eocene (Aldingan, Priabonian, planktonic foraminiferal zone P15). However, McGowran et al. (1997) placed the Tortachilla Limestone entirely within the late Middle Eocene (Johannian–Aldingan?, Bartonian, upper P14 and lower P15 foraminiferal zones). As parts of the lower unit of the Kingscote Limestone, the lower beds of the Muloowurtie Formation, and the upper Wilson Bluff Limestone (transitional to Toolinna Limestone) correlate in part with the Tortachilla Limestone, these sections may also be of late Middle Eocene age.

At Maslin Bay, an irregular unconformable contact exists between the Tortachilla Limestone and the overlying Blanche Point Formation (Cooper 1979), the lower member of which, the early Late Eocene Tuketja Member, is considered to lie in upper zone P15 (Langford et al. 1995; McGowran et al. 1997) or lower P16 (Lindsay & Alley 1995).

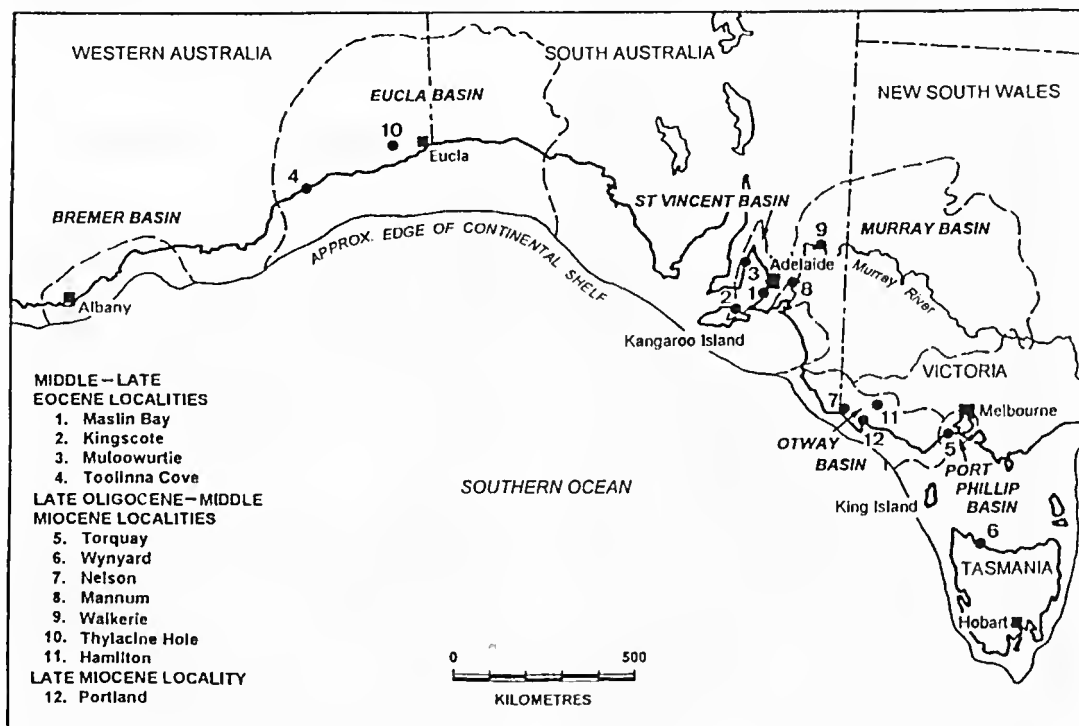


Fig. 1. Distribution of Middle-Late Eocene to Late Miocene fossil apatopygids in southern Australia.

Like the Tortachilla Limestone this member, although a calcareous mudstone, is also glauconitic and possibly the source of some echinoid specimens, including *A. vincentinus*, that have in the past been referred to the Tortachilla Limestone. Unfortunately as the exact stratigraphic horizon from which specimens have been collected is often unknown, the earliest and latest occurrence of *A. vincentinus* in the Middle–Late Eocene of southern Australia is still a matter of conjecture.

Although the Nanarup Limestone Member of the Werillup Formation, exposed in a small quarry at Nanarup, near Albany, Western Australia (Bremer Basin), contains an echinoid fauna similar to that of the Tortachilla Limestone, *A. vincentinus* has not yet been found (K. J. McNamara, pers. comm.).

Late Oligocene–Middle Miocene localities

Of Late Oligocene–Middle Miocene localities from which *Apatopygus* is recorded (Fig. 1, locs 5–11), only the Mannum Formation in the Murray Basin (Fig. 1, loc. 8), has yielded a significant number of specimens. The Jan Jue and Puebla Formations in the Port Philip Basin (Fig. 1, loc. 5), the Freestone Cove Sandstone on the margin of the Bass Basin (Fig. 1, loc. 6), the Gambier and Port Campbell Limestones in the Otway Basin (Fig. 1, locs 7 and 11), and the Abrakurrie Limestone of the Eucla Basin (Fig. 1, loc. 10), have so far yielded only rare specimens of the genus.

5. About 25 km southwest of Torquay, the oldest specimens of *Apatopygus mannumensis* so far recorded, have been found associated with numerous specimens of *Cassidulus? florescens* Gregory 1892 in yellowish sandy bryozoal calcarenite of the Late Oligocene–earliest Miocene? (Janjukian) Point Addis Limestone Member of the Jan Juk Formation, which crops out in coastal cliffs at Split Point, Aireys Inlet. Near the mouth of Spring Creek, Torquay, the Early Miocene Zeally Limestone Member of the Puebla Formation (Longfordian–?Batesfordian) is exposed in low cliffs at the back of the surf beach, about 200–300 m southwest of Point Danger, where *A. mannumensis* occurs with *Actapericulum bicarinatum* Holmes 1995 in a narrow band about 1 m above beach level.

6. Near Wynyard, on the north coast of Tasmania, a single poorly preserved specimen almost certainly attributable to *Apatopygus* has been found in the Early Miocene Freestone Cove Sandstone (Janjukian), the lower of the two calcareous marine formations of the Table Cape Group exposed at Fossil Bluff (Quilty 1972). The Freestone Cove

Sandstone and overlying Fossil Bluff Sandstone contain a unique, although sparse, echinoid fauna which includes *Echinolampas tatei* Lambert 1898, *Monostychia etleridgei* (Johnston 1877), and *Schizaster halli* McNamara & Philip 1980.

7. In southwestern Victoria, a small quarry in the Gambier Limestone, about 1.6 km north of Nelson, has yielded small poorly preserved echinoids that fit the general diagnosis of *Apatopygus*. These specimens are associated with the neolampadoids *Actapericulum bicarinatum* and *Notolampas flosculus* Philip 1963, and, based on the age of the Gambier Limestone outcrops in the vicinity, are Early Miocene (Longfordian–?Batesfordian) in age (Abele, pers. comm., in Kenley 1971). A single partial specimen, also probably *Apatopygus*, has been found in a quarry of similar age approximately 5 km northeast of Mount Gambier.

8. Specimens of *Apatopygus mannumensis* sp. nov. from the Mannum area, two-thirds of which were collected within 6 km of the town, are from the bioelastic calcareous sandstone and sandy limestone of the Early Miocene (Longfordian) upper Mannum Formation, exposed in road cuttings and cliffs along the Murray River between Wongulla and Mannum. In spite of an extremely rich echinoid fauna (Appendix 2), the only other cassiduloids recorded in the formation are *Cassidulus? florescens* (a single specimen), three species of *Echinolampas*, and *Studeria elegans* (Laube 1869), although both the neolampadoids *Actapericulum bicarinatum* and *Notolampas flosculus* are also present. Brown & Stephenson (1991), interpreted the Mannum Formation, Morgan Limestone and Pata Limestone as one lithological unit, the Mannum Limestone; the lower part encompassing the lower and upper Mannum Formation of Ludbrook (1961). This interpretation of the Mannum Limestone which includes the two marked biostratigraphic zones generally referred to as the Mannum Formation and Morgan Limestone (Appendix 2) was adopted by Rogers et al. (1995). However, Lukasik & James (1998) have now divided the Mannum Limestone, Murray Group of Ludbrook (1961) and Brown & Stephenson (1991), into six formations, retaining the original Mannum Formation as a separate lithological unit.

9. On the north side of the Murray River to the east of Waikerie, about 115 km northeast of Mannum, *Apatopygus mannumensis* sp. nov. and *Porterpygus devlinensis* sp. nov. occur in the upper Mannum Formation. Associated with large *Monostychia* sp., *Pericosmus compressus* (Duncan

1877) and *Studeria elegans*, as well as *Lovenia forbesii* (Tenison Woods 1862), *Ortholophus woodsi* (Laube 1869) and several brissid species, they occur in a strongly eroded soft limestone band about 4.5 m above the level of the river flats (R. J. Foster, pers. comm.).

10. Philip (1970) recorded *A. vincentinus* in the Late Eocene of the Eucla Basin and also noted its presence in the Early Miocene Abrakurrie Limestone at Thylacine Hole, just over 100 km east of Eucla. As the latter locality contains a Janjukian–Longfordian fauna, it is more than likely that the specimen listed by Philip is in fact *A. manmunensis*, although it has not been examined.

11. Richly fossiliferous brown and grey to dark grey silty marls of the Middle Miocene (Balcambian–Bairnsdalian) Muddy Creek Marl Member, a marginal member of the Port Campbell Limestone (Abele et al. 1988), crop out along the banks of Muddy Creek east of Hamilton, Victoria. These beds, although renowned for their rich molluscan fauna, also contain a diverse, but poorly recorded, echinoid fauna including *Apatopygus*. A single encrusted specimen has also been found in the underlying yellow brown to reddish brown limestone of the early Middle Miocene (Batesfordian) Bochara Limestone Member.

Age determination. *Apatopygus manmunensis* is recorded from the Late Oligocene–earliest Miocene (Janjukian, Chattian–Aquitian, planktonic foraminiferal zones P22?–N4) to at least the Middle Miocene (late Balcambian–early Bairnsdalian, Serravallian, zones N10–N12). Inconsistencies remain in recent publications concerning the stratigraphic range and correlation of Oligocene–Miocene formations with southeastern Australian regional stages and with international planktonic foraminiferal zones, particularly in the Australian Janjukian and Longfordian stages. However, McGowran et al. (1997) and Li et al. (1999) have gone some way towards rectifying these problems.

Late Miocene locality

12. A single 10.1 mm long specimen of *Apatopygus* found recently in the whitish chalky Late Miocene (Mitchellian, Tortonian) Port Campbell Limestone, in coastal cliffs northeast of Nun's Beach, Portland (Fig. 1, loc. 12), is the youngest known Australian Tertiary representative of the genus. This section of the Port Campbell Limestone corresponds to the upper part of the

planktonic foraminiferal zone N16 and the basal part of zone N17 (Singleton et al. 1976).

MATERIALS AND METHODS

Material on which this study is based is housed in Museum Victoria (specimen numbers prefixed NMV P) and the South Australian Museum (prefix SAM P). Some secondary material examined for statistical analysis and evidence of distribution is currently held in the private collections of F. C. and E. Holmes, C. AhYee and J. Krause, and A. Anderson. Measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL) followed by the mean, the standard deviation (SD) and the number of specimens measured (N).

SYSTEMATIC PALAEOONTOLOGY

Order CASSIDULOIDA Claus, 1880

Family APATOPYGIDAE Kier, 1962

Emended diagnosis. Test small to medium, longer than wide; apical system tetrabasal or monobasal, petals weakly or moderately developed, ambulacral plates beyond petals single pored, periproet supra-marginal in groove; bourrelets incipient to slightly developed, phylloids single pored with up to three rows of pores in each half ambulacrum, no buccal pores; demiplates (pyrinid plates) may be present in ambulacra beyond petals; no naked granular zone in interambulacrum 5. Triphyllous pedicellariae with a medium internal keel and dentate margin.

Genera and range. *Apatopygus* Hawkins, Late Paleocene to Recent; *Porterpygus* Baker, Early Miocene to Recent.

Remarks. While Australian fossil apatopygids generally fit Baker's (1983: 164) emended familial diagnosis, a further revision is necessary as *Apatopygus manmunensis* sp. nov. and the extant *A. occidentalis* Clark 1938 have relatively small tests, and *A. vincentinus* (Tate 1891) and the extant *A. recens* (Milne Edwards 1836) have the beginning of a third series of phylloid pores in one or both halves of the paired ambulacra. In addition, demiplates are variably present in fossil specimens and often restricted to the adoral surface. Lack of a naked granular zone adorally on the midline of interambulacrum 5 is considered to be a familial, rather than a generic trait.

Genus *Apatopygus* Hawkins, 1920

Type species. *Nucleolites reens* Milne Edwards, 1836 (extant) from New Zealand; original designation.

Emended diagnosis. Test small to medium, ovoid to subcircular at ambitus, low to moderately inflated; apical system tetrabasal or monobasal with four gonopores; petals narrow, open, usually conjugate; pyrinid plating in adoral and sometimes adapical ambulaera beyond petals: periproct supra-marginal in groove extending to posterior margin; peristome shallow to deep, bourrelets incipient to weakly developed, phylloides single pored, not widened, with two or possibly three series of pores in each half ambulacrum.

Remarks. This diagnosis accommodates the two fossil species, *A. vincentinus* and *A. mannumensis*, which are considerably more variable than the extant species on which previous diagnoses have been based.

Apatopygus vincentinus (Tate, 1891)

Figs 2A–J, 3A, D, F, 6H, 7A, D

Echinobrissus vincentinus Tate 1891: 280.—Gregory 1892: 435.

Cassidulus vincentinus (Tate).—Chapman 1915: 45.

Nucleolites vincentinus (Tate).—Clark 1946: 354 (part.).

Apatopygus vincentinus (Tate).—Philip in Lowry 1970: 183, (?non 186), pl. 5.—Holmes 1991: 19, figs 2D, 5A–B.

non *Apatopygus vincentinus* (Tate).—Sadler, Pledge & Morris 1983: 11.

Lectotype. SAM T266H from 'Aldinga', South Australia, the best preserved of Tate's eleven syntypes, is here chosen as lectotype.

Paralectotypes. SAM T266A–G and I from the type locality and SAM T266J and K from uncertain localities. SAM T266K is not conspecific with the rest of Tate's specimens but is a specimen of *A. mannumensis*.

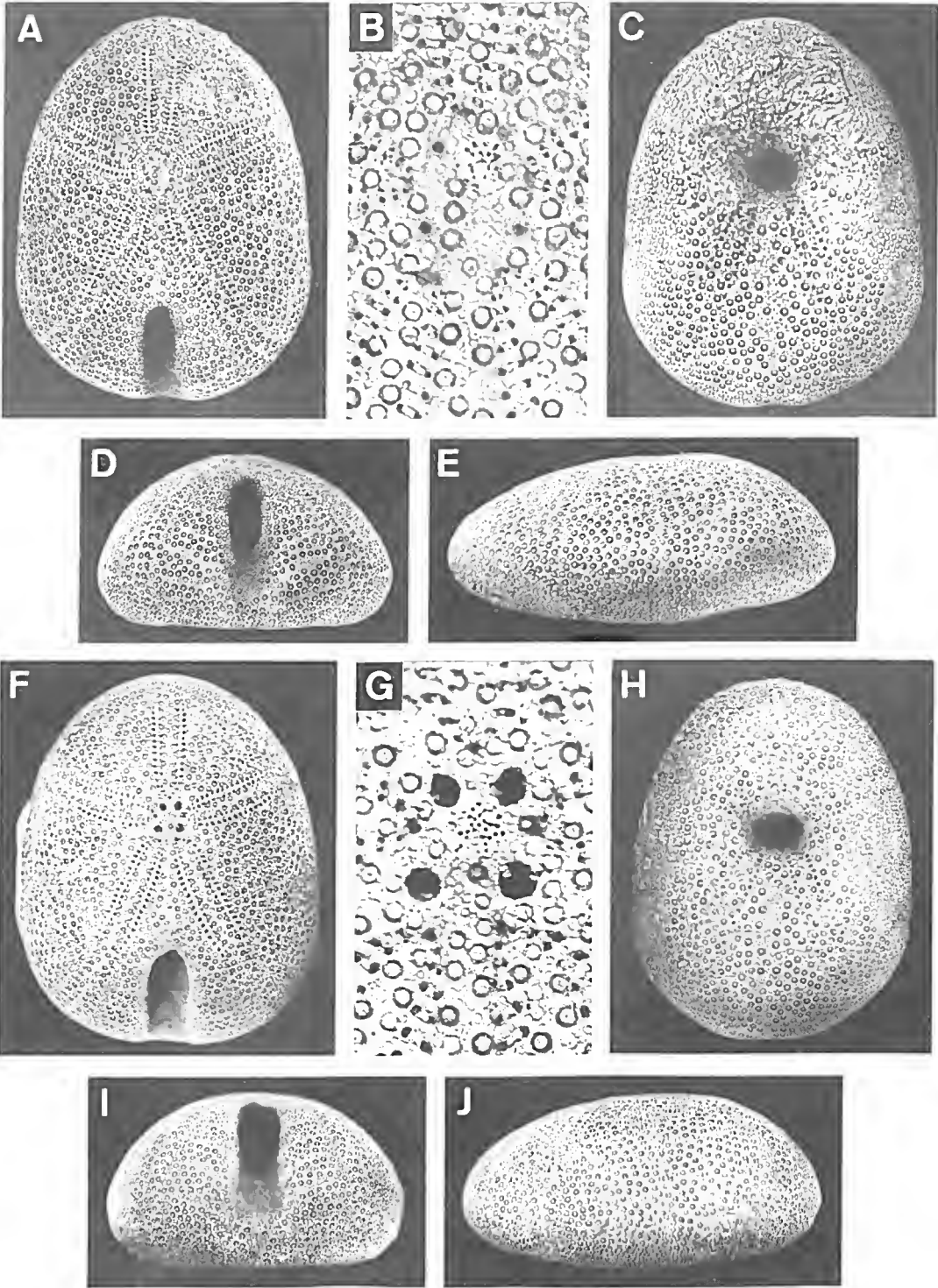
Other material. NMV P20220, 53186, 53189, 53190, 79371–79374, 82021, 82022 from 'Aldinga'; NMV P147943–147947 from 'Aldinga Bay'; NMV P133075, 148350–148362 from Maslin Bay; SAM P3328A–E from 'Aldinga Bay'; SAM P21955A–C, 22649A–C, 31804A and B, 35353A–E, 35355A and B from Maslin Bay; SAM P35354A and B purportedly from the River Murray eliffs but considered to be from Maslin Bay. Although a large number of specimens are registered as being from 'Aldinga' or 'Aldinga Bay', all specimens, including types (unless otherwise noted), are considered to be from the late Middle to early Late Eocene (Johannian–Aldingan, Bartonian–Priabonian) Tortachilla Limestone, north of Blanche Point, Maslin Bay. Tate's specimens SAM T266J and K were not used in statistical analysis.

The following separately analysed specimens from the lower unit of the late Middle to early Late Eocene (Johannian–Aldingan, Bartonian–Priabonian) Kingscote Limestone, Kingscote, Kangaroo Island, were used for comparative purposes: NMV P29501, 133074, 148363–148384; and SAM P35356A and B.

Diagnosis. Small to medium sized, low to moderately inflated, ovate with transversely concave adoral surface. Apical system and peristome anterior and equidistant from anterior ambitus. Petals moderately developed, paired petals extending about halfway to margin, unpaired petal three-fifths to two-thirds. Primary tubercles closely spaced adapically. Peristome deeply sunken, transversely elliptical to subpentagonal, marginally wider than long. Periproct elliptical, steeply angled and partly overhung by test at anterior end of long, deep, anal groove.

Description. Test 12.6–28.9 mm long (mean = 19.3 mm, SD = 3.6, N = 48), ovoid at the ambitus but with sides only narrowing slightly for about half the distance between the widest point and the anterior margin and with the posterior margin flattened or indented medially. Maximum width 69–84% TL (mean = 78.0%, SD = 3.0, N = 40) between 53–67% TL from the anterior ambitus (mean = 60.8%, SD = 2.9, N = 33), posterior to the apex and anterior to the anal groove. Aboral surface low to moderately inflated, transversely convex, gently curving upwards from evenly rounded anterior and lateral margins to a maximum height of 35–49% TL (mean = 41.8%, SD = 3.6, N = 33) between 50–62% TL from anterior ambitus (mean = 56.7%, SD = 3.1, N = 21). Between apex and posterior margin the aboral surface is more steeply curved, a few specimens tending to be obliquely truncated in the vicinity of the anal groove. Adoral surface slightly concave transversely between the anterior and posterior margins, mildly depressed around the well of the peristome, the degree of concavity depending on the extent of swelling of interambulacra 1 and 4 below the ambitus. Primary tubercles small, sunken, crenulate, perforate, closely spaced adapically and around margins with progressively wider spacing adorally towards peristome, particularly in interambulacrum 5.

Apical system, tetrabasal?, with four gonopores, centre situated 36–42% TL from anterior ambitus (mean = 37.6%, SD = 1.4, N = 29). Gonopores small; hydropores, situated proximal to gonopore 2, variable in number, maximum of 32 recorded in two specimens, 19.6 and 23.2 mm long. Ocular pores I and V furthest from centre of apical system.



Petals moderately developed, flush, fairly narrow, straight, open distally; posterior pair longest; anterior pair shortest. Posterior paired petals extending 44–57% of the radius (mean = 51.5%), measured from centre of apical system along perradial suture to the ambitus; anterior paired petals 45–61% of radius (mean = 53.2%); anterior unpaired petal 57–70% of radius (mean = 62.6%). Anterior paired petals diverge 130–148° (mean = 139°); posterior paired petals 300–316° (mean = 309°). Inner pore of pore pair round, outer pore round to marginally oval, pore pair spacing about 4 per millimetre, interporiferous zone 1.5–2.0 times width of pore pair. Maximum number of pore pairs 24 in ambulacra I and V, 19 in II, III and IV (specimen 22.1 mm long).

Phyllodes not expanded, only weakly developed; pores in shallow pits form biserial rows in each half ambulacrum in II, III and IV, tending to triserial in I and V; first pore in the inner series situated just inside the well above the peristome (Fig. 3A). A small number of closely spaced non-perforate pits also occur between the inner series of pores close to the peristome. Adoral plate structure of ambulacra visible on one or two specimens, with demiplates only evident on one of these (Fig. 3D). Incipient bourrelets present.

Peristome anterior, transversely elliptical to sub-pentagonal, with posterior edge slightly flattened, length 7–12% TL (mean = 8.1%, SD = 1.0, N = 23), width 9–13% TL (mean = 10.8%, SD = 0.9, N = 22), at base of moderately to deeply sunken well with granulated sides, 37–42% TL to centre from anterior ambitus (mean = 39.4%, SD = 1.1, N = 33).

Periproct 6–10% TL wide (mean = 8.2), longitudinally elliptical and angled at more than 45° to the horizontal at the anterior end of a deep anal groove, length 3.0–4.5 times width, extending to the posterior margin. Forward edge of periproct opening is below and anterior to the vertically visible end of the anal groove which is situated 61–75% TL from anterior ambitus (mean = 69.5%, SD = 3.6, N = 36). Base of the anal groove may rise above posterior edge of periproct opening before curving down to posterior margin.

Remarks. Statistical analysis is based solely on measurement of specimens from the type locality

at Maslin Bay. Specimens from Kingscote, Kangaroo Island, fall within the limits of the species but generally have a wider and higher test (Fig. 5B), less concave adoral surface, and marginally shorter anal groove with steeper angled periproct (Fig. 5D).

Apatopygus vincentinus is distinguishable from the extant type species *A. recens* by its more restricted size range, narrower test, more anterior apical system with fewer hydropores, and much narrower peristome. It also differs from the extant *A. occidentalis* by having shorter petals in ambulacra I and V, more widely spaced primary tubercles, a transversely elongated peristome, and a steeper angled periproct. *A. vincentinus* has greater anal groove length/width ratio, and far greater distance between the posterior margin and the posterior edge of the periproct than either extant species. It is also highly probable that the two species have different apical plate structures; *A. occidentalis* being described by Baker (1983) as monobasal, while an adult specimen of *A. vincentinus* from the Kingscote Limestone (Fig. 3F) and one from the Tortachilla Limestone clearly show a tetrabasal system.

The difference between *A. vincentinus* and *A. occidentalis* are based purely on a comparison with Baker's (1983) description, measurement and illustration of the latter.

In South Australia, *Apatopygus vincentinus* usually occurs with two other Late Eocene cassiduloids, *Australanthus longianus* (Gregory 1890) and *Eurhodia australiae* (Duncan 1877), that share many similar cassiduloid features. However, the latter forms are easily distinguished from *Apatopygus vincentinus* by their more posterior periproct, well developed phyllodes and bourrelets, and wide naked or pitted zone adorally on the midline of interambulacrum 5. A comparison with *A. mannumensis* sp. nov. is given below.

Apatopygus mannumensis sp. nov.

Figs 3B, E, 4A–E, 7B, E

Nucleolites vincentinus (Tate).—Clark 1946: 354 (part.).
Apatopygus vincentinus (Tate).—Sadlers, Pledge & Morris 1983: 11.

Fig. 2. *Apatopygus vincentinus* Tate. A, C–E, adapical, adoral, posterior and lateral views (×3.3), and B, detail of apical system (×13) of lectotype SAM T266H, from the Middle–Late Eocene Tortachilla Limestone, Aldinga Bay (Maslin Bay); F, I, J, adapical, posterior and lateral views (×3), and G, detail of apical system (×13) of NMV P148364, and H, detail of apical system of NMV P148370 from the Middle–Late Eocene Kingscote Limestone, Kingscote, Kangaroo Island.

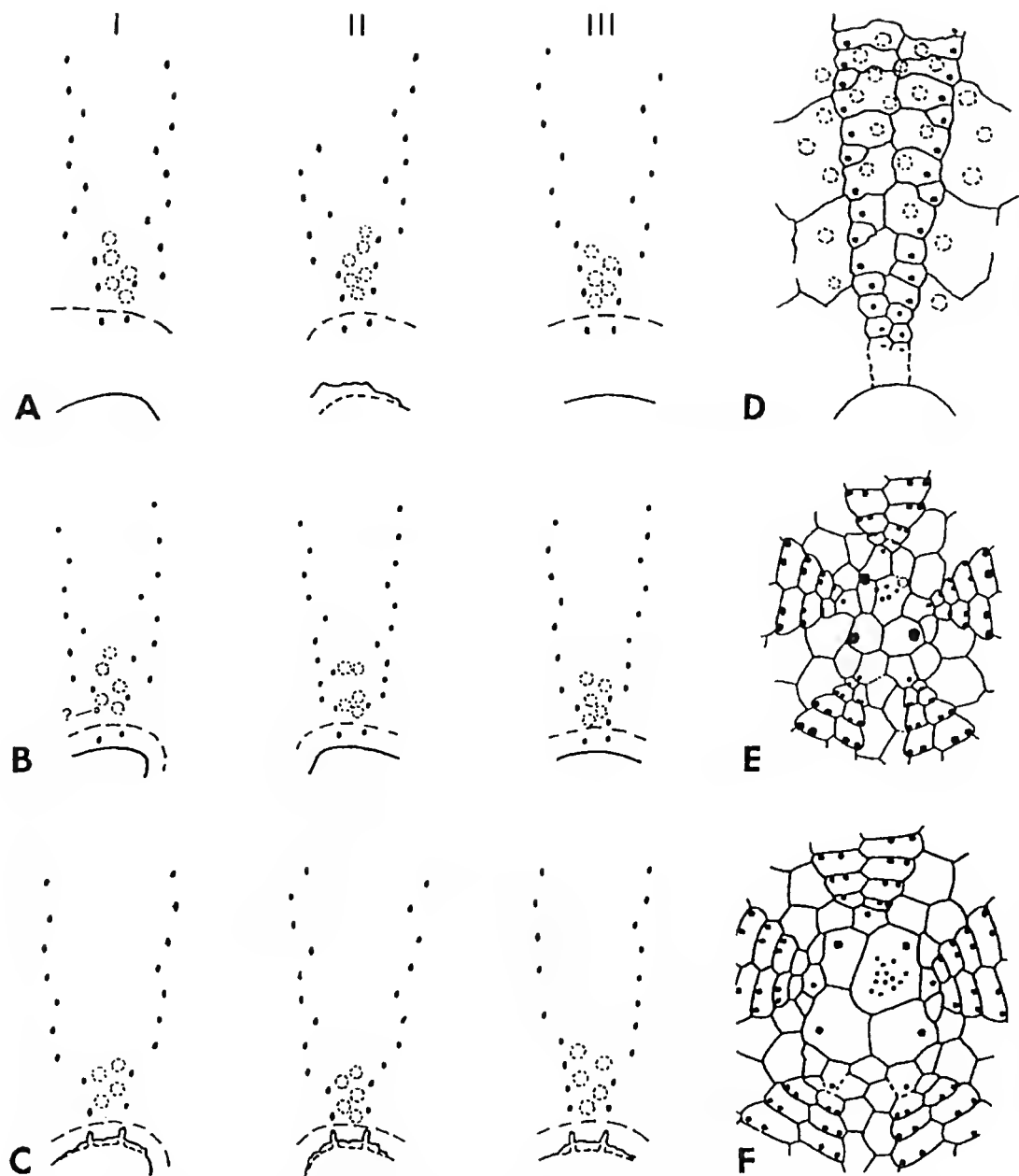


Fig. 3. A-C, phylloids pore arrangement in ambulacra I, II and III ($\times 12$); D, demiplate (pyramid) plate structure in adoral ambulacrum III ($\times 8$); and E and F, apical plate structure ($\times 16$). A, D, F, *Apatopygus vincentinus* (Tate); A, NMV P148362 and D, SAM T266D from the Middle-Late Eocene Tortachilla Limestone, Maslin Bay, and F, NMV P148377 from the Middle-Late Eocene Kingscote Limestone, Kangaroo Island. B, E, *A. mannumensis* sp. nov.; B, NMV P148496 and E, NMV P148391, from the Early Miocene Mannum Formation, near Mannum. C, *Porterpygus devlinensis* sp. nov.; NMV P148399, from the Early Miocene Mannum Formation, near Waikerie. In A-C, edge of recess above peristomal opening is indicated by long broken line and non-perforate pits by broken circles.

Etymology. From Mannum, a Murray River town near which the majority of specimens were collected.

Holotype. NMV P148496 from the Early Miocene (Longfordian, Aquitanian?–Burdigalian) Mannum Formation, Cowirra Swamp Road, near Mannum; collected by J. Krause and C. AhYee, April 1996.

Paratypes. NMV P148385 and 148386 from Coolcha Landing, Younghusband; NMV P148387 from Cauramont; NMV P148388 from Walker Flat; NMV P148389 and 148390 from Underwood Hill Road, Mannum; NMV P148391–148395 from side of road 3.4 km NE of Mannum. All from the Early Miocene Mannum Formation, South Australia.

Other material. Thirteen other specimens (currently held in private collections) from the Early Miocene Mannum Formation near Mannum.

The following separately analysed specimens were used for comparative purposes: NMV P148404 and 148405 from the Late Oligocene Jan Juc Formation, Point Addis Limestone Member, Aireys Inlet; NMV P148406–148408 from the Early Miocene Puchla Formation, Zeally Limestone Member, Point Danger, Torquay; NMV P148409–148411 from the Early Miocene Gambier Limestone, Nelson; and SAM P27908 from an unknown locality and horizon, Murray River cliffs.

Diagnosis. Small, moderately inflated, ovate, with transversely concave adoral surface. Apical system

and peristome anterior, the latter further from the anterior ambitus. Petals poorly developed, paired petals extend less than halfway to margin, unpaired petal just over halfway. Primary tubercles moderately spaced adapically. Peristome in shallow depression, transversely elliptical, wider than long. Periproct longitudinally elliptical, moderately angled at anterior end of long, shallow, anal groove.

Description. Test 9.1–14.5 mm long (mean = 11.3 mm, SD = 1.4, N = 23), elliptical to ovoid at the ambitus with posterior generally rounded and only rarely indented medially. Maximum width 74–82% TL (mean = 77.9%, SD = 1.9, N = 21) at 51–65% TL from the anterior ambitus (mean = 59.0%, SD = 3.5, N = 19), about halfway between the apex and the anterior end of the anal groove. Aboral surface mildly inflated, transversely convex, gently curving upwards from evenly rounded anterior and lateral margins but flattening out in vicinity of apex. Maximum height 37–48% TL (mean = 43.2%, SD = 2.8, N = 21) at 48–56% TL from anterior ambitus (mean = 53.6%, SD = 1.7, N = 16). Aboral surface evenly curved between apex and posterior margin. Adoral surface mildly concave transversely between anterior and posterior margins, slightly depressed around the peristome.

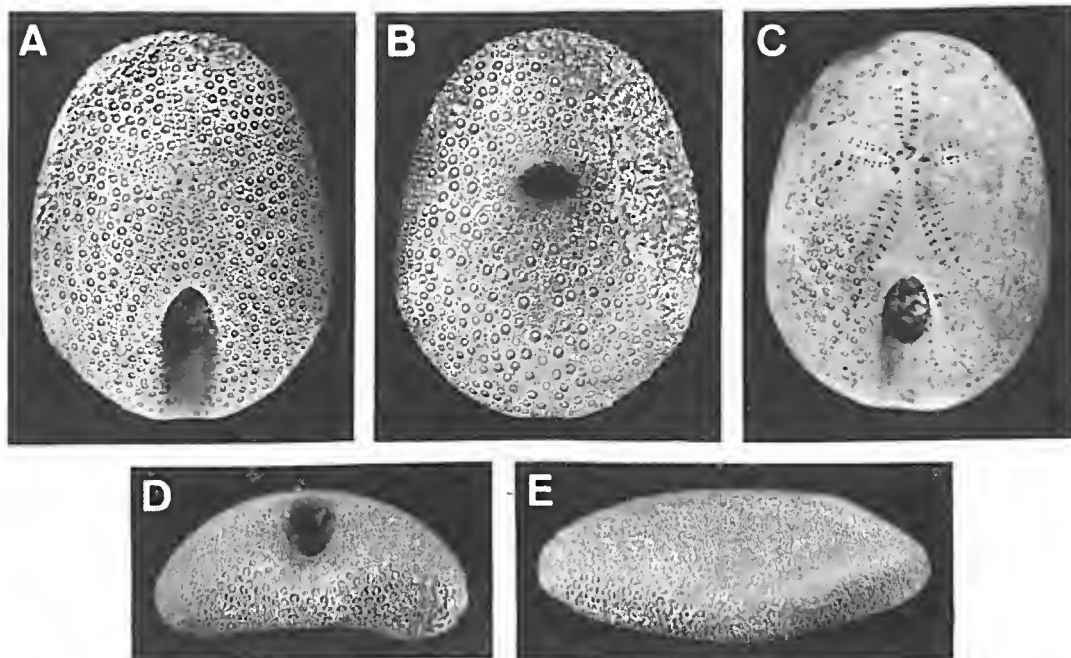


Fig. 4. *Apatopygus mannunensis* sp. nov. A, B, D, E, adapical, adoral, posterior and lateral views ($\times 4$) of holotype NMV P148496, and C, adapical view ($\times 5.5$) of paratype NMV P148393 from the Early Miocene Mannum Formation, near Mannum.

Primary tubercles moderately small, sunken, crenulate, perforate, fairly widely and evenly spaced over the whole test, marginally further apart adorally.

Apical system, anterior, centre situated 33–38% TL from anterior ambitus (mean = 35.3%, SD = 1.2, N = 15). A tetrabasal (ethmophract) apical system plate arrangement, visible on only one 13.1 mm long specimen (Fig. 3E), with 4 medium sized gonopores and large pierced ocular plates, posterior pair, I and V, in contact with each other. Specimens show 5–12 hydropores proximal to gonopore 2.

Petals flush, narrow, short, straight, open distally; posterior pair longest; anterior pair shortest. Posterior paired petals 41–53% of radius (mean = 45.6%), measured from centre of apical system along the perradial suture to the ambitus; anterior paired petals 38–54% of radius (mean = 46.3%); anterior unpaired petal 47–65% of radius (mean = 55.3%). Anterior paired petals diverge 138–153° (mean = 145°); posterior paired petals 306–312° (mean = 309°). Pores round; pore pair spacing about 4 per millimetre, interporiferous zone 1.5–2.0 times width of pore pair. Maximum number of pore pairs 17 in ambulacra I and V, 12 in II and IV, and 13 in III (specimen 13.1 mm long).

Phyllodes not expanded, barely developed; pores in shallow pits form biserial rows in each half ambulacrum with the first pore of the inner series just inside the slight depression around the peristome (Fig. 3B). A small number of closely spaced non-perforate pits occur between the inner series of pores close to the peristome. Adoral plate structure of the ambulacra is unknown. Bourrelets incipient.

Peristome anterior, transversely elliptical, sometimes with lateral edges pointed and posterior edge slightly flattened, length 7–11% TL (mean = 9.0%, SD = 1.0, N = 15), width 11–16% TL (mean = 13.0%, SD = 1.3, N = 17), situated in shallow depression 38–42% TL to centre from anterior ambitus (mean = 39.4%, SD = 1.1, N = 198).

Periproct longitudinally elliptical, with anterior edge sometimes pointed, horizontally 12–19% TL long (mean = 16.5%), 8–13% TL wide (mean = 10.8%); opening angled 30–40° to the horizontal at the anterior end of a long shallow anal groove with length 2.8–4.0 times width, extending to the posterior margin. Anterior end of anal groove 58–67% TL from anterior ambitus (mean = 63.5%, SD = 2.5, N = 21).

Remarks. Statistical analysis used in the description is based on specimens collected from the vicinity of the Murray River between Walker Flat and Mannum (Mannum Formation). Other

separately analysed Late Oligocene and Early Miocene specimens from near Torquay (Jan Juc and Puebla Formations), and from Nelson (Gambier Limestone), are comparable with the new species, showing only very minor variations in periproct size and anal groove length.

Although previously considered a small form of *A. vincentinus*, *A. mannumensis* differs by having relatively shorter petals in ambulacra II, III and IV, and relatively longer petals in I and V; more divergent anterior paired petals; more evenly and wider spaced primary tubercles; a shallow, marginally wider and often transversely pointed peristome; and a much longer, shallower anal groove with a wider and lower angled periproct, not anteriorly overhung by the test (Fig. 7E).

Like *A. vincentinus* it differs from extant *A. occidentalis* in anal groove length and distance of periproct from the posterior margin. In addition *A. mannumensis* has a less posteriorly located maximum test width and, unlike *A. occidentalis*, does not have a semicircular peristome or very closely spaced primary tubercles.

A. mannumensis has a strong superficial resemblance to the small neolampadid *Actapericulum bicarinatum* with which it is sometimes found; however, the latter species is recognisable by well developed bourrelets and a lack of petals.

Genus *Porterpygus* Baker, 1983

Type species. *Porterpygus kieri* Baker, 1983 (extant) from near Three Kings Islands, New Zealand; original designation.

Diagnosis. See Baker (1983: 164)

Porterpygus devlinensis sp. nov.

Figs 3C, 6A–G, 7C, F

Etymology. From Devlins Pound, an early settlers' trap for mustering horses on the river flats, near where the specimens were found.

Holotype. NMV P148399 from the Early Miocene (Longfordian) Mannum Formation exposed in cliffs on the right bank of the Murray River about 16 km east of Waikerie (NMV PL3430).

Paratypes. NMV P148396–148398, 148400 and 148401 from the type locality.

Diagnosis. Small to medium, low, ovate, with transversely concave adoral surface. Apical system and peristome anterior, the former much closer

to the anterior ambitus than the latter. Petals moderately developed, comparatively long, flush, fairly narrow; paired petals extending three-fifths

distance to margin, unpaired petal just over two-thirds. Primary tubercles closely and evenly spaced. Peristome in shallow depression, transversely sub-

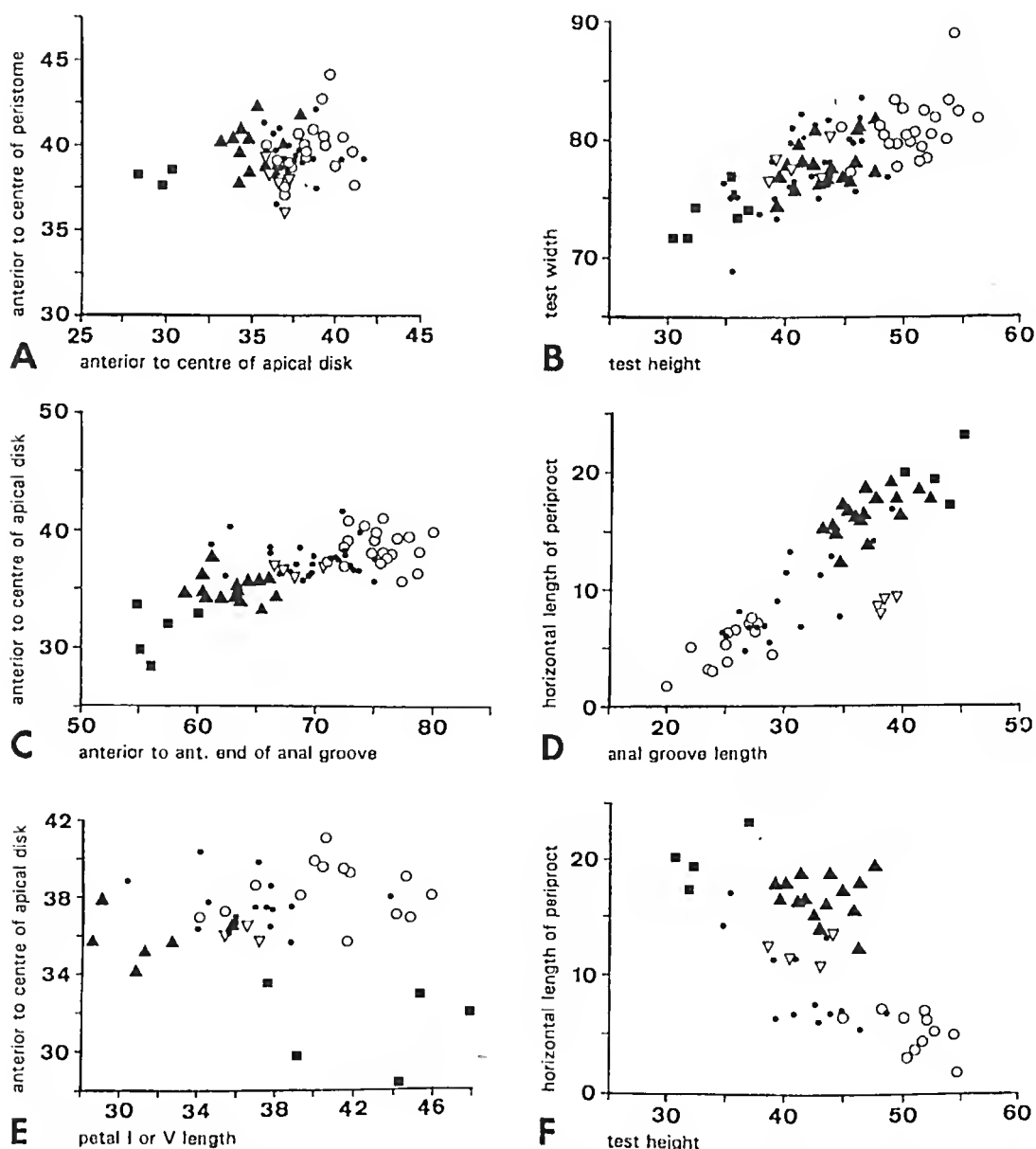


Fig. 5. Comparative biometric data on specimens of *Apatopygus vincentinus* (Tate) from the Middle-Late Eocene Tortachilla Limestone, Maslin Bay (•), and Kingscote Limestone, Kangaroo Island (○); *A. mannumensis* sp. nov. from the Early Miocene Mannum Formation, near Mannum (▲), and the Late Oligocene-earliest Miocene Jan Juc and Late Early Miocene Puebla Formations, near Torquay (▽); and *Porterpygus devlinensis* sp. nov. from the Early Miocene Mannum Formation, near Waikerie (■). Both vertical and horizontal scales show data as a percentage of the specimens test length.

circular to subpentagonal, slightly wider than long. rounded ends, moderately angled at anterior end
Periproct longitudinally elliptical with sharply of a very long, wide, shallow anal groove.

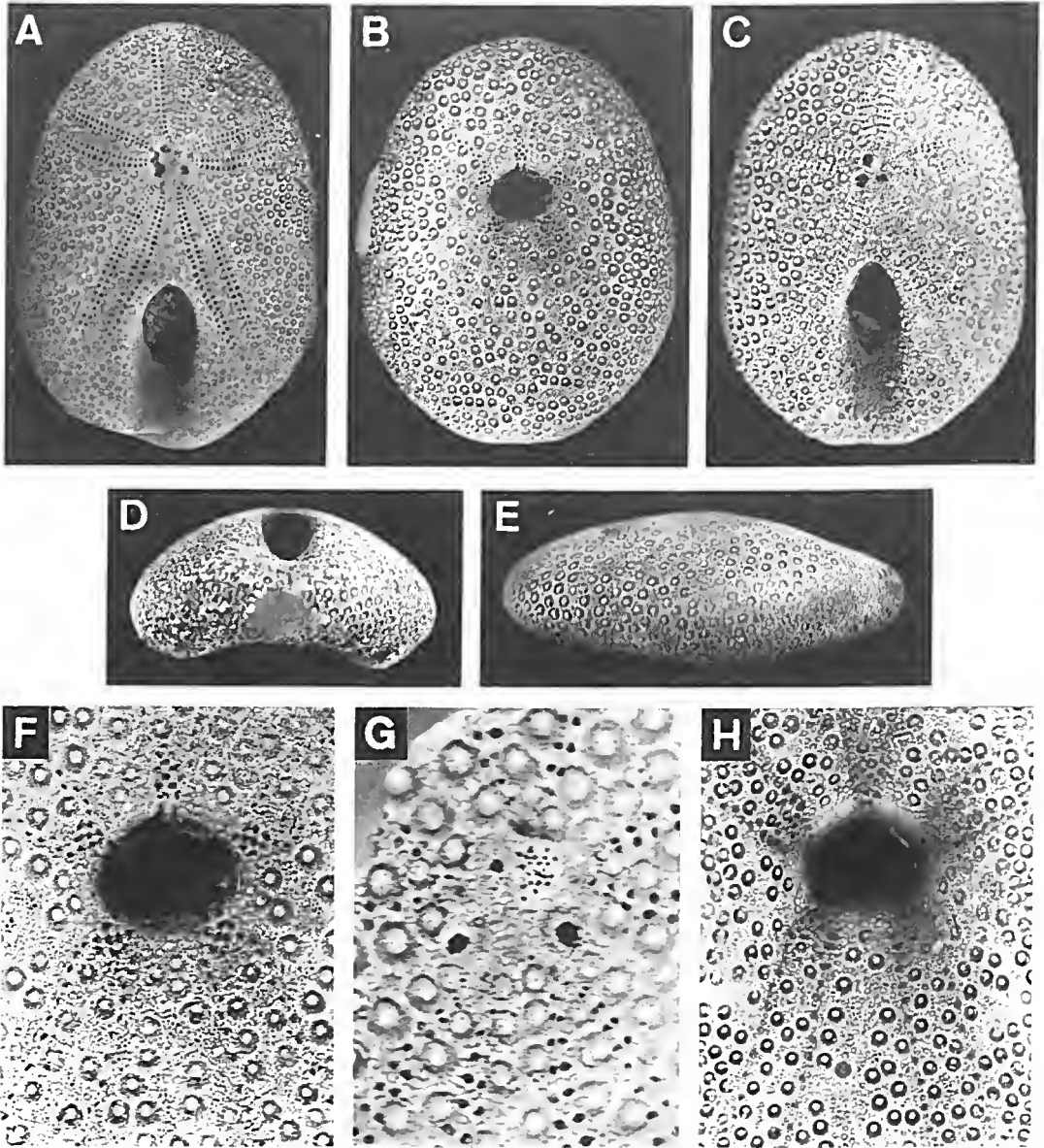


Fig. 6. *Porterpygus devlinensis* sp. nov. A, adapical view ($\times 2.4$) of paratype NMV P148396; B, adoral view ($\times 3$) and F, detail of peristomal area ($\times 7$) of holotype NMV P148399; C, D, adapical and posterior views ($\times 4$) of paratype NMV P148401; E, lateral view ($\times 3.5$) of paratype NMV P148400; and G, detail of apical system ($\times 12$) of paratype NMV P148398. All from the Early Miocene Mannum Formation, near Waikerie. *Apatopygus vincentinus* Tate. H, detail of peristomal area ($\times 4.5$) of NMV P79374 from the Middle-Late Eocene Tortachilla Limestone, Aldinga Bay (?Maslin Bay).

Description. Test 14.6–24.3 mm long (mean = 19.3 mm, SD = 3.5, N = 6), ovoid at the ambitus but with posterior margin flattened or indented medially. Maximum width 72–77% TL (mean = 73.6%, SD = 1.6, N = 6) at 56–65% TL from anterior ambitus (mean = 59.8%, SD = 2.9, N = 6)

just posterior to the anterior end of the anal groove. Aboral surface low, transversely convex, gently curving upwards from sharply rounded anterior and lateral margins. Maximum height 32–37% TL (mean = 35.1%, SD = 1.9, N = 4) at 44–54% TL from anterior ambitus (mean = 49.2%, SD = 3.5,

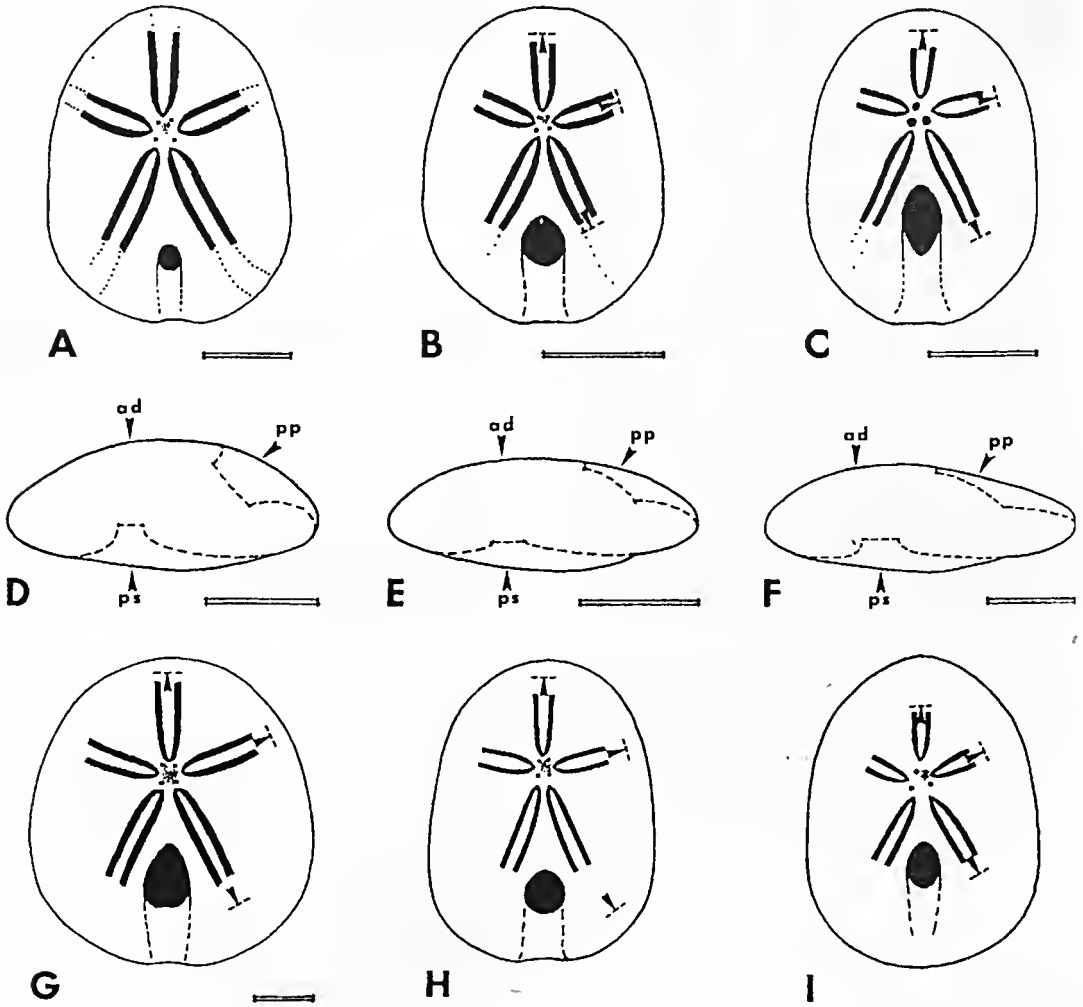


Fig. 7. Comparative drawings of fossil and recent apatopygids in adapical (A–C, G–I) and lateral (D–F) views; scale bars 5 mm. *Apatopygus vincentinus* (Tate), A, SAM T266H and D, NMV P147947, from the Middle–Late Eocene Tortachilla Limestone, Maslin Bay; *A. mannumensis* sp. nov., B and E, NMV P148496, from the Early Mioecene Mannum Formation, near Mannum; *Porterpygus devlinensis* sp. nov., C, NMV P148401 and F, NMV P148399, from the Early Mioecene Mannum Formation, near Waikerie; *Apatopygus recens* (Milne Edwards), G, recent from New Zealand; *A. occidentalis* Clark, H, recent from Western Australia; *Porterpygus kieri* Baker, I, recent from New Zealand. Arrows on adapical views show approximate maximum recorded petal lengths of species (where greater than specimen figured); broken lines and arrows on lateral views indicate centre of apical disk (ad), periproctal recess (pp) and peristomal recess (ps). Figs H and I adapted from Baker (1983).

N = 4). Between the apex and the sharply rounded posterior margin the aboral surface is mildly truncate in the vicinity of the anal groove. Adoral surface mildly concave transversely between the edges of the anterior and posterior margins and in addition slightly depressed around and posterior to peristome. Primary tubercles small, sunken, crenulate, perforate, moderately close and evenly spaced overall but with closer spacing just below the ambitus and wider spacing in depression around peristome.

Apical system with three gonopores, centre between 28–34% TL from anterior ambitus (mean = 31.2%, SD = 1.8, N = 6). Although gonopores 1, 3 and 4 are present, 4 sometimes posterior to 1, due to poor preservation the apical plate structure can only be tentatively described as tetrabasal. Hydropores variable in number, with a maximum of 23 in a specimen 20.1 mm long, situated proximal to interambulaerum 2. Large gonopores in two out of the six known specimens, suggests dimorphism.

Petals flush, fairly narrow, generally straight, mildly divergent in ambulaerum III, and open distally. Posterior paired petals much longer than others (mean = 42% TL), anterior pair (mean = 25% TL) only marginally shorter than unpaired petal (mean = 25% TL). Anterior pair of petals diverging at 146–156° (mean = 151°), posterior pair at 308–314° (mean = 310°). Pores round; pore pairs approximately 3 per mm, interporiferous zone about twice the width of the pore pair. Maximum number of pore pairs 26/27 in ambulaera I and V, 17/18 in ambulaera II, III and IV (specimen 24.3 mm long).

Phyllodes not expanded, barely developed, single pores tend to form uniserial rows in each half ambulaera I, III and V, but biserial rows in II and IV; first pore in each half ambulaerum just outside the slight depression around the peristome. Narrow slits, in line with the two rows of pores between the weakly developed bourrelets, occur in the edge of the test around the peristome opening (Fig. 3C). Between the rows of pores close to the peristome are a small number of non-perforate pits. Adoral plate structure of ambulaera not known.

Peristome anterior, subcircular to subpentagonal, slightly wider than long, centre about 38% TL from anterior ambitus.

Periproct longitudinally elliptical, with anterior and posterior ends sharply rounded, about 20% TL long and 12% TL wide, angled 30–35° to the horizontal at the anterior end of a very long, wide and shallow, anal groove which just reaches the posterior margin. Anterior end of anal groove 55–60% TL from anterior ambitus (mean = 56.8%,

SD = 1.9, N = 5), posterior edge of periproct 20–26% TL (mean = 22.8%, SD = 2.4, N = 4) from posterior margin.

Remarks. *Porterpygus devlinensis* sp. nov. is only the second recorded species of the genus and the first from the fossil record. While superficially very similar to the extant type species *P. kieri*, it differs in having a far more anterior apical system, a shallower less anterior peristome, considerably longer petals, a steeper angled periproct, and a less sharply rounded posterior margin (Fig. 7C). Its three gonopores and much longer posterior paired petals distinguish it from the Early Miocene *Apatopygus mannumensis*, with which it occurs in the upper Mannum Formation.

DISCUSSION

The tetrabasal apical system in what must be considered adult specimens of the Late Paleocene–Early Eocene *Apatopygus* sp. from the Chatham Islands, New Zealand (*A. aff. recens* of Brighton 1929: 311, fig. 2); the Middle–Late Eocene *A. vincentinus*, and the Late Oligocene–Middle Miocene *A. mannumensis* from South Australia (Fig. 3E, F); support the suggestion by Suter (1994h), in a cladistic analysis of living eassiduloids, that the ontogenetic character of the apical system in the extant *A. recens* (tetrabasal in immature specimens, monobasal in adults) is derived. Further, Mooi (1990: 70, fig. 1) figured an adult specimen of *A. recens* over 40 mm long with a tetrabasal apical system in which each of the four genital plates contain multiple hydropores. However, this latter configuration appears suspect, particularly in view of the figures published by Mortensen (1921: 187, fig. 21a, b) which infer that the ontogenetic fusing of the plates, leading towards a monobasal system, follows the development of the madreporite. Whether the development of the apical system of the small extant Australian species *A. occidentalis* is similar to *A. recens* is unknown, no immature specimens having been recorded.

This evidence, together with the occurrence of a tetrabasal apical system in the Early Miocene *Porterpygus devlinensis* and the extant *P. kieri*, refutes the statement made by Kier (1962) that eassiduloids rapidly changed from a tetrabasal to a monobasal system in the Late Cretaceous and that such a change was (in adult specimens) all inclusive.

That nucleolitids are ancestral to the apatopygids has never been seriously disputed, Kier (1962) having erected the latter family only because the

apatopygids have single pores and pyrinid plating in the ambulaera beyond the petals, features, with the partial exception of *Oolopygus*, not found in nucleolitids. Mortensen (1948) even considered 'the great stress laid by Hawkins (1920) on the ambulaeral structure, particularly the so-called "Pyrinid" structure', to be greatly exaggerated; a fact supported by this study. Smith (1984: fig. A.1) showed the Nucleolitidae extending from the earliest Middle Jurassic to the present day, presumably to incorporate the Apatopygidae, a family which he does not mention or include in his classification of the Echinoidea.

Although Suter (1994a) noted that the results of cladistic analyses of cassiduloid phylogeny are ambiguous and analysis of morphological characters demonstrate extensive, but not excessive, homoplasy among cassiduloid genera, his figured consensus trees and cladograms, in particular his preferred phylogenetic hypothesis, closely link the apatopygids (based on the characteristics of the three extant species) with a small group of Cretaceous–Early Paleogene nucleolitids. From this cladistic evidence, Suter concluded that the extant apatopygids are a small remnant of the same paraphyletic stem group to more recent clades (e.g. the cassidulid, faujiid echinolampadid and neolampadid–oligopygoid–clypeasteroid clades).

Morphological variation within fossil apatopygids is fairly pronounced between groups of specimens from different populations (Fig. 5) making any definitive link between fossil and extant species a matter for speculation. However, the

three southern Australian species of *Apatopygus* probably constitute a single lineage, although there are no distinct evolutionary trends evident, with the exception of a general decrease in size and reduction in the number of hydropores. Indeed, based on some characteristics it is possible that the extant *A. occidentalis* is more closely related to the Middle–Late Eocene *A. vincentinus* than to the Late Oligocene–Middle Miocene *A. mannumensis*.

The relationship between Australian and New Zealand species of the genus is even more difficult to postulate. Suter (1994b) concluded that *Apatopygus* is probably not monophyletic. There is little evidence that the extant *A. recens* is a descendant of either of the two fossil species, even though the Australian Early Miocene *Porterpygus devlinensis* and the New Zealand extant *P. kieri*, each found associated with *Apatopygus*, seem to be very closely related.

Confirmation of *Apatopygus*, *Giraliaster* and *Echinolampas* in the Late Paleocene–Early Eocene strata of the Chatham Islands (Campbell et al. 1993), echinoids comparable with those found in the Middle–Late Eocene of southern Australia (Fig. 8), raises further questions as to the early diversification of *Apatopygus*, particularly as the Chatham Island occurrence pre-dates that in Australia by more than 12 million years. While this occurrence and that of the eidarid *Eucidaris*, which is also found in the Chatham Islands, represent the first record of these genera, *Giraliaster* first appears in the Middle Paleocene

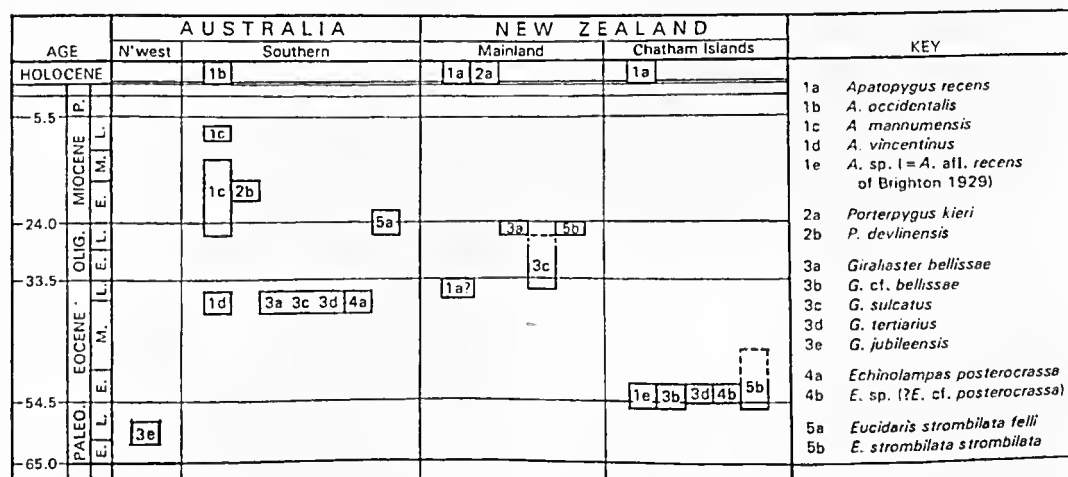


Fig. 8. Stratigraphic range of apatopygids in the Cenozoic of Australia and New Zealand compared with that of echinoid genera known to occur in the Late Paleocene–Early Eocene strata of the Chatham Islands. Data based on Foster & Philip (1978), Baker (1983), Campbell et al. (1993) and current research (see text).

Cardabia Formation of the Carnarvon Basin, Western Australia (K. J. McNamara, pers. comm.) and *Echinolampas* in the Paleocene–Early Eocene of North Africa, Pakistan and Madagascar (Roman 1965).

Except for a single schizasterid species found subsurface in the Perth Basin (McNamara 1993), there is no record of the southern Australian Paleocene–Early Eocene echinoid fauna that must have existed. Outcrops of marine sediments from this period of time are restricted to the Late Paleocene Pebble Point Formation in the Otway Basin of Victoria which, although containing a fairly rich molluscan fauna, is devoid of echinoids (T. A. Darragh, pers. comm.). Without such a record it is impossible to say whether the Chatham Islands echinoids are, at least in part, linked to any southern Australian fauna as the result of intermittent trans-Tasman migration during the Paleocene–Early Eocene; well before the accelerated opening of the oceanic gap between Australia and Antarctica and the onset of major marine transgressions over continental margins that commenced in the late Middle Eocene. The first substantiated easterly trans-Tasman migration of echinoids took place during the early–mid Tertiary; two species of *Giraliaster* from the Middle–Late Eocene of southern Australia also being recorded from the latest Eocene–Oligocene of mainland New Zealand (Foster & Philip 1978).

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REFERENCES

- ABELE, C., KENLEY, P. R., HOLDGATE, G. & RIPPER, D., 1988. Otway Basin. In *Geology of Victoria*, Victorian Division, Geological Society of Australia Incorporated, Melbourne, 272–303.
- BAKER, A. N., 1983. A new apatopygid echinoid genus from New Zealand (Echinodermata: Cassiduloida). *National Museum of New Zealand Records* 2(15): 163–173.
- BRIGHTON, A. G., 1929. Tertiary irregular echinoids from

- the Chatham Islands, New Zealand. *Transactions and Proceedings of the New Zealand Institute* 60(2): 308–319, pl. 30.
- BRIGHTON, A. G., 1930. A Tertiary irregular echinoid from the Chatham Islands, New Zealand. *Transactions and Proceedings of the New Zealand Institute* 60(4): 565–570.
- BROWN, G. M. & STEPHENSON, A. E., 1991. Geology of the Murray Basin southeastern Australia. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 235: 1–430.
- CAMPBELL, H. J. ET AL., 1993. Cretaceous–Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand. *Institute of Geological and Nuclear Sciences Monograph* 2: 1–269 + map.
- CHAPMAN, F. A., 1915. Report on a collection of fossils made by Dr A. Wade from the Cainozoic Series of South Australia, Appendix 2. In *The supposed oil bearing areas of South Australia*, A. Wade, ed. *Geological Survey of South Australia Bulletin* 4: 44–50.
- CLARK, H. L., 1938. Echinoderms from Australia. *Memoir of the Museum of Comparative Zoology, Harvard* 55: viii + 596 pp, 28 pls.
- CLARK, H. L., 1946. The echinoderm fauna of Australia, its composition and its origin. *Carnegie Institute of Washington, Publication* 566: 1–567.
- COOPER, B. J., 1979. Eocene to Miocene stratigraphy of the Willunga Embayment. *Department of Mines and Energy, Geological Survey of South Australia, Report of Investigations* 50: 1–101.
- DUNCAN, P. M., 1877. On the Echinodermata of the Australian Cainozoic (Tertiary) deposits. *Quarterly Journal of the Geological Society of London* 33: 42–73, pls 3–4.
- EDWARDS, M. MILNE, 1836. Les Zoophytes ou animaux rayonnés. In *Le Règne Animal distribué d'après son Organisation, pur servir de base à l'histoire naturelle des animaux, et d'introduction à l'anatomie comparée* (3rd edn), George Cuvier, ed., Fortin, Masson et Cie, Libraires, Paris, 190 pp, 97 pls.
- FOSTER, R. J. & PHILIP, G. M., 1978. Tertiary holasteroid echinoids from Australia and New Zealand. *Palaenology* 21(4): 791–822, pls 85–93.
- GREGORY, J. W., 1890. Some additions to the Australian Tertiary Echinoidea. *The Geological Magazine* 27: 481–492, pls 13–14.
- GREGORY, J. W., 1892. Further additions to Australian fossil Echinoidea. *The Geological Magazine* 29: 433–437, pl. 12.
- HALL, T. S. & PRITCHARD, G. B., 1896. Remarks on the proposed subdivision of the Eocene rocks of Victoria. *Proceedings of the Royal Society of Victoria* 8: 151–168.
- HAWKINS, H. L., 1920. Morphological studies on the Echinoidea, Holcetypoida and their allies. X. On *Apatopygus* gen. nov. and the affinities of some recent Nucleolitoida and Cassiduloida. *The Geological Magazine* 57: 393–401, pl. 7.
- HOLMES, F. C., 1991. Australian Tertiary cassiduloids—an overview (pt 1). *The Fossil Collector* 34: 11–27.

- HOLMES, F. C., 1993. Australian fossil echinoids: annotated bibliography and list of species. *Occasional Papers from the Museum of Victoria* 6: 27–54.
- HOLMES, F. C., 1995. Australian Tertiary Neolampadidae (Echinoidea): a review and description of two new species. *Proceedings of the Royal Society of Victoria* 107(2): 113–128.
- IRWIN, R. P., 1995. New family and genus of Clypeasteroidea (Echinoidea) from the Australian Tertiary. *Memoirs of the Association of Australasian Palaeontologists* 18: 189–198.
- IRWIN, R. P. & ARCHIBOLD, N. W., 1994. The spatangoid echinoid *Lovenia* from the Tertiary of southeastern Australia. *Proceedings of the Royal Society of Victoria* 106: 1–15.
- JOHNSTON, R. M., 1877. Further notes on the Tertiary marine beds of Table Cape. *Papers and Proceedings and Report of the Royal Society of Tasmania for 1876*: 79–90f.
- KENLEY, P. R., 1971. Cainozoic geography of the eastern part of the Gambier Embayment, south-western Victoria. In *The Otway Basin of southeastern Australia* (Special Bulletin of the Geological Surveys of South Australia and Victoria), H. Wopfner & J. G. Douglas, eds, Government Printer, Adelaide, 89–153.
- KIER, P. M., 1962. Revision of the cassiduloid echinoids. *Smithsonian Miscellaneous Collections* 144(3): 1–262, pls 1–44.
- KIER, P. M., 1966. Cassiduloids. In *Treatise on Invertebrate Paleontology, Part U, Echinodermata* 3 (2 vols), R. C. Moore, ed., The Geological Society of America Inc. and The University of Kansas Press, U492–523.
- LAMBERT, J., 1898. Echinoderms. *Review critique de Paleozoologie* 2(4): 163–167.
- LAMBERT, J. & THIÉRY, P., 1925. *Essai de nomenclature raisonnée des échinides* 6 & 7. Librairie L. Ferrière, Chaumont, 385–512, pls 10–11, 14.
- LAMBERT, J. & THIÉRY, P., 1924. *Essai de nomenclature raisonnée des échinides* 8 & 9. Librairie L. Ferrière, Chaumont, 513–607, pls 12–13, 15.
- LANGFORD, R. P., WILFORD, G. E., TRUSWELL, E. M. & ISERN, A. R., 1995. *Palaeogeographic Atlas of Australia, Vol. 10—Cainozoic*. Australian Geological Survey Organisation, Canberra, i–iv, 1–37.
- LAUBE, G. C., 1869. Über einige fossile Echiniden von den Murray Cliffs in Süd-Australien. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften zu Wien* 59: 183–198, figs 1–8.
- LI, Q., DAVIES, P. J. & MCGOWRAN, B., 1999. Foraminiferal sequence biostratigraphy of the Oligo-Miocene Janjikian strata from Torquay, southeastern Australia. *Australian Journal of Earth Sciences* 46: 261–273.
- LINDSAY, J. M. & ALLEY, N. F., 1995. St. Vincent Basin. In *The geology of South Australia, Vol. 2, The Phanerozoic*, J. F. Drexel & W. V. Preiss, eds, *Geological Survey of South Australia, Bulletin* 54: 163–172.
- LUDBROOK, N. H., 1961. Stratigraphy of the Murray Basin in South Australia. *Geological Survey of South Australia, Bulletin* 38: 1–96, pls 1–8.
- LUKASIK, J. J. & JAMES, N. P., 1998. Lithostratigraphic revision and correlation of the Oligo-Miocene Murray Supergroup, western Murray Basin, South Australia. *Australian Journal of Earth Sciences* 45: 889–902.
- MCGOWRAN, B., LI, Q. & MOSS, G., 1997. The Cenozoic neritic record in southern Australia: the biogeohistorical framework. In *Cool-water carbonates*, N. P. James & J. Clarke, eds, *Society of Economic Palaeontologists and Mineralogists, Special Publication* 56: 185–203.
- MCMANARA, K. J., 1993. First record of a spatangoid echinoid from the Palaeocene of the Perth Basin, Western Australia. *Records of the Western Australian Museum* 16(3): 331–336.
- MCMANARA, K. J. & BARRIE, D. J., 1992. A new genus of marsupiate spatangoid from the Miocene of South Australia. *Records of the South Australian Museum* 26(2): 139–147.
- MCMANARA, K. J. & PHILIP, G. M., 1980. Australian Tertiary schizasterid echinoids. *Alcheringa* 4(1): 47–65.
- MILNES, A. R., LUDBROOK, N. H., LINDSAY, J. M. & COOPER, B. J., 1983. The succession of Cainozoic marine sediments on Kangaroo Island, South Australia. *Transactions of the Royal Society of South Australia* 107: 1–15.
- MOOI, R., 1990. Living cassiduloids (Echinodermata: Echinoidea): a key and annotated list. *Proceedings of the Biological Society of Washington* 103(1): 63–85.
- MORTENSEN, T., 1921. Echinoderms of New Zealand and the Auckland-Campbell Islands. I, Echinoidea. Papers from Dr T. Mortensen's Pacific Expedition 1914–1916, viii. *Videnskabelige Meddelelser Dansk naturhistorisk Forening* 73: 139–197, 8 pls.
- MORTENSEN, T., 1948. A monograph of the Echinoidea 4(1). *Holcypoida, Cassiduloida*. C. A. Rietzel, Copenhagen, 371 pp, 14 pls.
- PHILIP, G. M., 1963. Two Australian Tertiary neolampadids, and the classification of cassiduloid echinoids. *Palaeontology* 6: 718–726, pls 106–107.
- PHILIP, G. M., 1970. Tertiary echinoids from the Eucla Basin. Appendix 1. In *Geology of the Western Australian part of the Eucla Basin*, D. C. Lowry, ed. *Bulletin of the Geological Survey of Western Australia* 122: 182–191, pl. 5.
- QUILTY, P. G., 1972. The biostratigraphy of the Tasmanian marine Tertiary. *Papers and Proceedings of the Royal Society of Tasmania* 106: 25–44.
- ROGERS, P. A., LINDSAY, J. M., ALLEY, N. F., BARNETT, S. R., LABLACK, K. L. & KWITKO, G., 1995. Murray Basin. In *The geology of South Australia, Vol. 2, The Phanerozoic*, J. F. Drexel & W. V. Preiss, eds, *Geological Survey of South Australia, Bulletin* 54: 163–172.
- ROMAN, J., 1965. Morphologie et évolution des Echinolampas (Echinides Cassiduloides). *Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre* 15: 1–341, pls 1–12.

- SADLER, T., PLEDGE, N. S. & MORRIS, B., 1983. *Fossils of South Australia. Pt 1: Sea urchins of the Murray River cliffs*. Quoll Enterprises, Seaton, South Australia, xxx + 34 pp.
- SINGLETON, O. P., McDougall, I. & MALLETT, C. W., 1976. The Pliocene-Pleistocene boundary in south-eastern Australia. *Journal of the Geological Society of Australia* 23: 299-311.
- SMITH, A., 1984. *Echinoid Palaeobiology*. George Allen & Unwin, London, xii + 190 pp and fig. 1A.
- STUART, W. J. JNR, 1970. The Cainozoic stratigraphy of the eastern coastal area of Yorke Peninsula, South Australia. *Transactions of the Royal Society of South Australia* 94: 151-178, figs 2-4.
- SUTER, S. J., 1994a. Cladistic analysis of cassiduloids: trying to see the phylogeny for the trees. *Biological Journal of the Linnean Society* 53: 31-72.
- SUTER, S. J., 1994b. Cladistic analysis of the living cassiduloids (Echinoidea), and the effects of character ordering and successive approximations weighting. *Zoological Journal of the Linnean Society* 112: 363-387.
- TATE, R., 1891. A bibliography and revised list of the described echinoids of the Australian Eocene, with descriptions of some new species. *Transactions and Proceedings and Report of the Royal Society of South Australia* 14: 270-282.
- WANG, C.-C., 1994. Phylogenetic analysis of the fossil-asterid echinoids (Order Clypeasteroidea) from Australia. *Journal of the Geological Society of China* 37(2): 225-246.
- WOODS, J. E. Tenison, 1862. *Geological observations in South Australia: principally in the district south-east of Adelaide*. Longman, Green, Longman, Roberts & Green, London, xviii + 404 pp.

Appendix 1. Middle-Late Eocene echinoids recorded from the Tortachilla Limestone (St Vincent Basin), South Australia.

Cidaroida

- Stereocidaris cudmorei* Philip 1964
S. fosteri Philip 1964
S. interius Philip 1964
S.? *hispidus* Philip 1964
S.? *intricata* Philip 1964
S. sp. 'C' Philip 1964

Salenoida

- Salenidia tertiaria* (Tate 1877): Philip 1965

Temnopleuroidea

- Ortholophus bitueneri* Philip 1969
Tatechinus nudus Philip 1969

Clypeasteroidea

- Fibularia gregata* Tate 1885

Cassiduloida

- Apatopygus vincentius* (Tate 1891)
Australanthus longianus (Gregory 1890)
Echinolaupas posterocrassa Gregory 1890: McNamara & Philip 1980
Eurhodia australiae (Duncan 1877): Philip 1970

Neolampadoida

- Aphanopora?* *bassoris* Holmes 1995: Holmes, unpub. ident.
Pisolaupas coucinna Philip 1963

Holasteroidea

- Giraliaster bellissae* Foster & Philip 1978
G. sulcatus (Hutton 1873): Foster & Philip 1978
G. tertius (Gregory 1890): Foster & Philip 1978

Spatangoida

- Gillechinus cudmorei* Fell 1963: McNamara, Philip & Kruse 1986
Hemiasper (Bolbaster) subidus McNamara 1987
Linthia pulchra McNamara 1985
Prenaster aldingensis Hall 1907: Philip 1970
Proteuaster preaustralis McNamara 1985
Psephoaster lissos McNamara 1987
Schizaster (Paraster) tatei McNamara & Philip 1980
-

Appendix 2. Early-Middle Miocene echinoids recorded from the Mannum Formation and Morgan Limestone (Murray Basin), South Australia. Man. = Mannum Formation; Mor. = Morgan Limestone; *? = occurrence of species in the formation, although noted in past literature, needs to be confirmed.

	Man.	Mor.
Cidaroida		
<i>Delocidaris prunispinosa</i> (Chapman & Cudmore 1928), var. 'A' radioles of Philip 1964	*	*
<i>Goniocidaris murrayensis</i> Chapman & Cudmore 1934; Philip 1964	*?	*
<i>Goniocidaris?</i> <i>pentaspinosa</i> Chapman & Cudmore 1928, var. 'B' radioles of Philip 1964	*	*
<i>Phyllacanthus clarki clarki</i> (Chapman & Cudmore 1934); Philip 1963		*
<i>Menocidaris compta</i> Philip 1963	*?	*
Arbacioida		
<i>Murravechinus paucituberculatus</i> (Gregory 1890): Philip 1965	*?	*
Temnopleuroidea		
<i>Cryptechinus humilior</i> (Bittner 1892): Philip 1963		*
<i>Goniosigma murrayensis</i> (Philip 1969)	*	*
<i>Goniosigma princeps</i> (Philip 1969)	*	
<i>Ortholophus morganensis</i> Philip 1969		*
<i>Ortholophus pulchellus</i> (Bittner 1892): Philip 1969		*
<i>Ortholophus woodsi</i> (Laube 1869): Philip 1969	*	
<i>Paradoxechinus novus</i> Laube 1869; Philip 1969 and Philip & Foster 1971	*	
<i>Paradoxechinus profundus</i> Philip & Foster 1971	*?	
Echinoida		
<i>Heliocidaris ludbrookae</i> Philip 1965	*	
<i>Strongylocentrotus antiquus</i> Philip 1965	*	
Clypeasteroida		
<i>Clypeaster</i> sp.: Holmes, unpub. ident.		*
<i>Fibularia gregata</i> Tate 1885	*	*?
<i>Monostychia australis</i> Laube 1869	*	*
<i>Monostychia</i> sp. 'A': Sadler, pers. comm.	*	
<i>Monostychia</i> sp. 'B': Sadler, pers. comm.	*	
<i>Monostychia</i> sp. 'C': Sadler, pers. comm.		*
<i>Prowillungaster major</i> Wang 1994	*	
<i>Scutellinoides patella</i> (Tate 1891): Irwin 1995	*?	*
<i>Sismondia?</i> <i>murravica</i> Tate 1893	*?	*
<i>Willungaster scutellaris</i> Philip & Foster 1971; Holmes, unpub. ident.	*	
Cassiduloida		
<i>Apatopygus mannumensis</i> sp. nov.	*	
<i>Cassidulus?</i> <i>florescens</i> Gregory 1892; Holmes, unpub. ident.	*	
<i>Echinolampas gambierensis</i> Tenison Woods 1867; McNamara & Philip 1980	*	
<i>Echinolampas morgani</i> Cottcau 1890; McNamara & Philip 1980	*	
<i>Echinolampas ovulum</i> Laube 1869; McNamara & Philip 1980	*	
<i>Porterpygus devlinensis</i> sp. nov.	*	
<i>Stnderia elegans</i> (Laube 1869)	*	*?
Neolampadoida		
<i>Actapericulum bicarinatum</i> Holmes 1995	*	
<i>Notolampas flosculus</i> Philip 1963	*	
Holasteroida		
<i>Corystus dysasteroides</i> (Duncan 1877): Foster & Philip 1976b	*	

	Man.	Mor.
Spatangoida		
<i>Amoraster tuberculata</i> McNamara & Ah Yee 1989	*	
<i>Brissopsis tatei</i> Hall 1907; McNamara, Philip & Kruse 1986		*
<i>Brissus fosteri</i> McNamara, Philip & Kruse 1986	*	
<i>Cyclaster archeri</i> (Tenison Woods 1867): McNamara, Philip & Kruse 1989	*	*
<i>Eupatagus cetus</i> Kruse & Philip 1985	*	
<i>Eupatagus collabus</i> Kruse & Philip 1985	*	
<i>Eupatagus ludbrookae</i> Kruse & Philip 1985	*	*
<i>Eupatagus murrayensis</i> Laube 1869: Kruse & Philip 1985	*	
<i>Eupatagus rotundas</i> Duncan 1877: Kruse & Philip 1985	*	*
<i>Eupatagus wrighti</i> Laube 1869: Kruse & Philip 1985		*
<i>Hemiasiter (Bolbaster) planedeclevis</i> Gregory 1890: McNamara 1987a		*
<i>Hysteraster paragrapsinus</i> McNamara & Barrie 1992		*
<i>Lovenia forbesii</i> (Tenison Woods 1862): Irwin & Archbold 1994	*	*?
<i>Lovenia woodsii</i> (Etheridge 1875): Irwin & Archbold 1994		*?
<i>Pericosinus compressus</i> (Duncan 1877): McNamara & Philip 1984	*	*?
<i>Pericosinus celsus</i> McNamara & Philip 1984	*	
<i>Pericosinus</i> sp. 'A' McNamara & Philip 1984	*	
<i>Protenaster autiaustralis</i> (Tate 1885): McNamara 1985	*	
<i>Psephoaster klydonos</i> McNamara 1987	*	
<i>Schizaster (Dipneustes) fosteri</i> McNamara & Philip 1980	*	
<i>Schizaster (Schizaster) abductus</i> Tate 1891: McNamara & Philip 1980		*
<i>Victoriaster gigas</i> (McCoy 1882): McNamara & Philip 1984		*?

Note: References to authors and supporting literature cited in the above appendices, but not listed in the main text references, can be found in Holmes (1993).

ADDITIONAL RECORDS OF PERMIAN BRACHIOPODS FROM NEAR RAT BURI, THAILAND

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ARCHBOLD, N. W., 1999:07:31. Additional records of Permian brachiopods from near Rat Buri, Thailand. *Proceedings of the Royal Society of Victoria* 111(1): 71–86. ISSN 0035-9211.

The Permian brachiopod fauna of three localities from northern Peninsular Thailand is documented and new records are described. Two new subgenera of *Neochonetes* Muir-Wood 1962 are recognised and named: *Neochonetes (Nongtaia)* and *Neochonetes (Zechiella)*. The new species *Neochonetes (Nongtaia) taoni* is described. The ages of the Permian brachiopod faunas of Peninsular Thailand are reviewed and the assemblages described herein are referred to the Ufimian (=Roadian) stage.

Key words: Brachiopoda, Permian, Peninsular Thailand, Rat Buri Limestone, *Neochonetes*.

BRACHIOPODS are often abundant in the Permian marine fossil faunas of Peninsular Thailand. The collections described herein were briefly reported on by Baird et al. (1993) and Baird & Bosence (1993) based on initial determinations made by the present author. Baird et al. (1993) noted that the brachiopods identified for their study were from three localities and they grouped the three assemblages together for purposes of biostratigraphy. The present study separates the three assemblages, illustrates the species present and provides descriptions of the new records.

STRATIGRAPHY AND LOCALITIES

The Permian stratigraphy of Peninsular Thailand consists of a complex of siliclastic rocks, at times with prominent lithic fragments, overlain by the extensive Rat Buri Limestone.

The stratigraphy of the siliclastic sedimentary sequence is complex. An elaborate and confusing series of names has been applied to various stratigraphical sections from numerous geographical regions of the outcrop as summarised in the comprehensive reports by Stokes (1975) and Raksaskulwong & Wongwanich (1993, 1994). Portion of the historical use of various names is summarised in Table 1, the sources for which are Raksaskulwong & Wongwanich (1993: 5 and 1994: 112–114). The Kaeng Kraehan (or Phuket) Group includes horizons informally known as the 'pebbly mudstones'. Considerable debate has occurred con-

cerning the depositional environment of the 'pebbly mudstones' with some authors favouring a debris flow and turbidity current model of deposition (eg. Mitchell et al. 1970; Garson et al. 1975; Sawata et al. 1975; Altermann 1986) while others favour a glacial origin or influence on the sequence (eg. Stauffer 1983; Stauffer & Mantajit 1981; Metcalfe 1985, 1990, 1993, 1995; Ingavat-Helmeke & Helmeke 1994; Mantajit 1978, 1999).

The Rat Buri Limestone, deposited in a shelf or platform setting, overlies the Kaeng Kraehan Group, either unconformably (Brown et al. 1951) or conformably (Bunopas 1976), and may interdigitate with the top beds of the Kaeng Kraehan Group (Stokes 1975). Two small assemblages described herein were collected from quartzites from immediately below the carbonate sequence.

The three assemblages documented herein were collected by Dr Angus Baird, then of the Department of Geology, Royal Holloway and Bedford New College, University of London, Surrey, England, during 1989, who also provided the following locality data (Figs 1, 2).

Assemblage A1: Khao Nong Ta On—from a prominent brachiopod rich horizon at the top of the lower siliclastic sequence, just below the Rat Buri Limestone.

Assemblage B1: Khao Sam Ngan—from a locality midway in the carbonate section, Rat Buri Limestone.

Assemblage C1: Khao Bat Kwang—from beds immediately above a brachiopod rich horizon at the top of the siliclastic sequence, just below the Rat Buri Limestone.

Mitchell et al. 1970	Piyasin 1976	Garson et al. 1975	Pitakpaivan & Mantajit 1981	Raksaskulwong & Wongwanich 1993
Rat Buri Limestone	Rat Buri Limestone	Rat Buri Limestone	Rat Buri Group	Rat Buri Group
Upper Fm with Bryozoa	Khao Chao Fm	Upper Fm with Bryozoa and brachiopods	Ko Yao Noi Fm	Khao Phra Fm
Lower Fm	Khao Phra Fm	Lower Fm		Ko He Fm
	Huai Phu Noi Fm			Spillway Fm
				Khao Wang Kradot Fm

Table 1. Names applied to stratigraphical units below the Rat Buri Limestone.

PREVIOUS BRACHIOPOD FAUNAL STUDIES OF PENINSULAR THAILAND AND THEIR AGES

Brachiopod faunas have previously been described or illustrated from the Kaeng Krachan Group (including the pebbly mudstones) by Hamada (1960), Garson et al. (1975) and Waterhouse (1981a, 1982). Two distinct faunas have been documented. The apparently older fauna described by Hamada (1960) and Waterhouse (1982) consists of species of the genera *Arctitreta*, *Komukia*, *Bandoproductus*, *Rhynchopora*, *Sulcipleca*, *Spirelytha*, *Lanniplica* and *Elasmata*. Originally assigned to the Carboniferous (Hamada 1960) the fauna was later assessed as Late Asselian (Waterhouse 1982). While lacking such characteristic cold water genera as the bivalve genus *Eurydesma*, five of the constituent genera out of nine (*Arctitreta*, *Bandoproductus*, *Rhynchopora*, *Sulcipleca* and *Spirelytha*) are shared with Late Asselian? or Tastubian (Early Sakmarian) and Sterlitamakian (Late Sakmarian) faunas of Australia (Archbold & Shi 1995; Shi & Archbold 1995). A sixth genus (*Lanniplica*) is shared with comparable faunas from Peninsular India (in addition to *Bandoproductus* and a possible *Rhynchopora*)—see Archbold et al. (1996). Briggs (1998) provides a detailed analysis of the genus *Bandoproductus* and noted the wide variability of the Thailand species described by Hamada (1960) and Waterhouse (1982). On

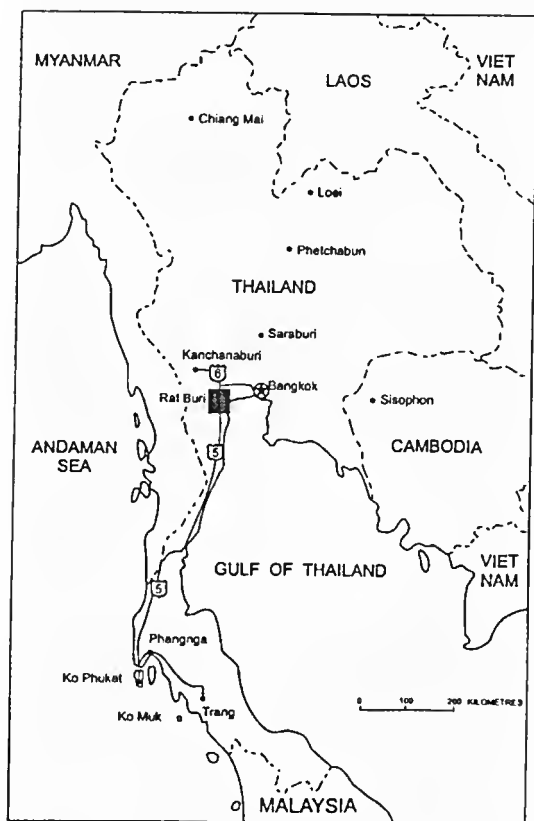


Fig. 1. Location map of the Rat Buri Area of north Peninsular Thailand.

balance, a Late Asselian or more likely, a Tastubian age is the preferred age estimate for this fauna.

A possibly allied fauna of Sterlitamakian age, from Langkawi Island, Peninsular Malaysia was briefly described by Shi et al. (1997). Several species of the Malaysian assemblage (eg. those

of *Bandoproductus*, *Rhynchopora*, *Sulcipleca* and *Spirelytha*) are close to those described by Waterhouse (1982) but a martiniid is present in the Langkawi fauna. Although referred to *Spinomartinia* by Shi et al. (1997), confirmation of the presence of the external ornament of

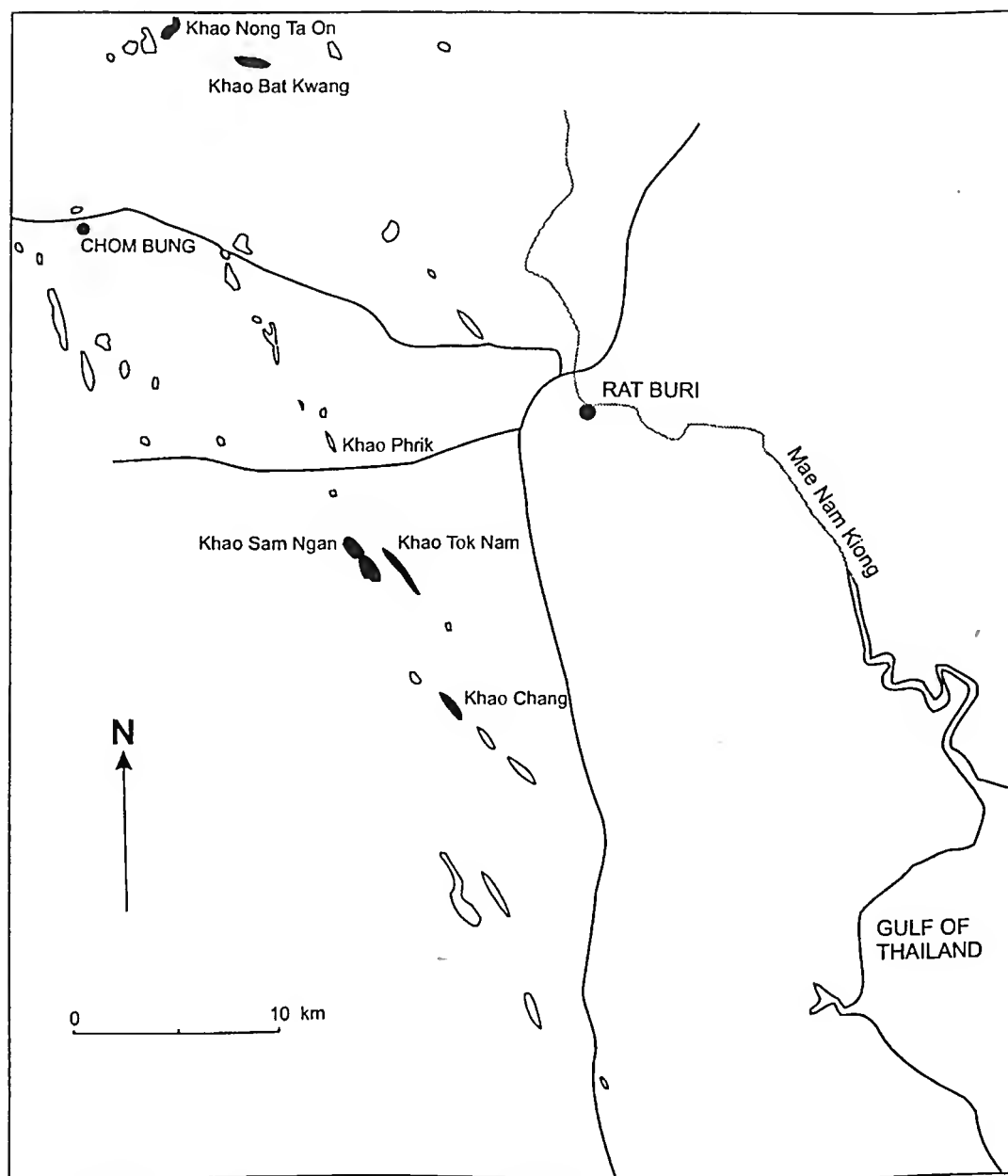


Fig. 2. Map of the Rat Buri Area showing outcrops of Rat Buri Limestone. Named outcrops are in black.

fine spinules is required for confident recognition of the genus (Waterhouse 1981a: 107). A Late Sakmarian or early Artinskian fauna from the Baoshan block, western Yunnan (Fang 1994) also includes *Bandoproductus* and a possible *Sulciplica* in addition to *Globiella*.

A younger, much more diverse, fauna has been mentioned by Young & Jantaraniya (1970), partially figured by Garson et al. (1975) and described by Waterhouse (1981a). The fauna, from beds high in the Ko Yao Noi Formation, 'could be Sakmarian or as young as Baigendzhinian' although 'likely to be Sakmarian' according to Waterhouse (1981a: 124). The fauna includes representatives of genera that characterise the Upper Byro Group of the Carnarvon Basin, Western Australia, such as *Demonedys*, *Dyschrestia*, *Retimarginifera*, *Spiriferella* and *Spirelytha* and hence suggests a younger age than Sakmarian (Sterlitamakian and Aktastinian in the sense of Waterhouse, 1981a). Also noteworthy are the numerous generic links with the brachiopod faunas of the lower Rat Buri Limestone (Waterhouse 1981a: 120) although species are distinctive. In view of the recent modifications to the ages assigned to the Western Australian late Early Permian stratigraphical units (i.e. the recognition of an extended Kungurian record) as discussed by Archbold (1998a, 1998b) and the current views on the age of the brachiopod faunas of the Peninsular Rat Buri Limestone (see below) it appears increasingly likely that the upper Kaeng Krachan fauna described by Waterhouse (1981a) may be Late Artinskian (Baigendzhinian) in age.

The brachiopod faunas of the Rat Buri Limestone of peninsula Thailand (the latter geographical region defined by Fontaine et al. 1994a) were first recorded by G. A. Cooper in Brown et al. (1951: 35) and have been progressively well described by Waterhouse & Piyasin (1970), Yanagida (1971) and Grant (1976) with ages also discussed by Piyasin (1975), Waterhouse (1973, 1976, 1981b) and Yanagida (1984). All of these authors recognised to some degree a mid-Permian (Kungurian to Late Ufimian = Roadian in the current terms) element to the faunas, although the then knowledge of the mid-Permian subdivisions of the timescale hampered precise dating. Links were recognised with the Bituani fauna of Timor, the Amb fauna of the Salt Range, Pakistan and the Road Canyon Formation of West Texas, all of mid-Permian age. Recent discussions on the age of several of these units indicates an age range of Bolorian (Kungurian) and Kubergandian (Ufimian including Roadian) as indicated by Fontaine et al. (1994), Angiolini et al. (1998) and Iqbal et al. (1998). In terms of the timescale used by Archbold (1998a,

1998b) an Ufimian age is assigned by me to the Peninsular Rat Buri Limestone brachiopod faunas. Permian crinoids from the Rat Buri Limestone are, in general terms, also consistent with this age assignment (cf. Webster & Jell 1993; Racey et al. 1994) as are elements of the distinctive coral faunas of Peninsular Thailand (Fontaine et al. 1994b). A correlative fauna is known from Irian Jaya (Indonesia) as described and discussed by Archbold (1981a, 1992) and Archbold et al. (1982) and commented on by Fontaine et al. (1994b). It should be noted that studies based on small foraminiferids and other microfloras and faunas often indicate ages younger than Ufimian (Kubergandian–Roadian) for outcrops of the Rat Buri Limestone (eg. see Baird et al. 1993; Baird & Bosence 1993; Dawson et al. 1993; Fontaine et al. 1994). However, the brachiopod faunas come from low in the Limestone which 'has not yielded microfaunas or (has) provided very poor microfaunas without stratigraphical meaning' (Fontaine et al. 1994: 136).

THE NEW COLLECTIONS

The species identified herein are listed in Table 2. Each assemblage is identified separately. Preservation of the specimens is as silicified replacements and minute surface details and features such as punctae are preserved. Figured specimens are housed in the collections of the Museum of Victoria, Melbourne (NMV P). All species are figured but only new species and records are described.

The assemblages from Khao Nong Ta On and Khao Sam Ngan share the species *Orthotichia waterhousei*, *Waterhouseiella speciosa* and *Spiriferellina adunctata*. This indicates that the two assemblages can be correlated. The additional species of the two assemblages, consisting of *Marginifera otaria*, *Cleiothyridina seriata*, *Hustedia ratburiensis* and *Notothyris triplax*, confirm a correlation with the Rat Buri Limestone faunas as described by Waterhouse & Piyasin (1970), Yanagida (1971) and Grant (1976). Of interest are the new records of chonetids *Neochonetes (Nongtaia) taoni* sp. nov. and *Quinquenella?* sp., from Khao Nong Ta On. These indicate that the Rat Buri faunas have yet to yield their full diversity.

The assemblage from Khao Bat Kwang is more difficult to assess. The orthotetid fragments are not diagnostic and the *Trigonotreta* specimen is the first record of the genus from Thailand although it is considered by the present author that several of the specimens, assigned to *Neospirifer*

sterlitamakensis (Gerasimov, 1929) by Waterhouse (1981a) from the Kaeng Krachan Group, Ko Yao Noi Formation, belong to a group of *Trigonotreta* species well developed in the Sterlitamakian to Ufimian faunas of Western Australia (Arehbold & Thomas 1986) and elsewhere in peripheral Gondwanan regions. *Trigonotreta* has yet to be identified from the Rat Buri Limestone proper and hence may indicate a somewhat older age for the Khao Bat Kwang occurrence.

SYSTEMATIC PALAEONTOLOGY

Order CHONETIDA Nalivkin, 1979

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETOIDEA Bronn, 1862

Family RUGOSOCHONETIDAE
Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE
Muir-Wood, 1962

Genus *Neochonetes* Muir-Wood, 1962

Subgenus *Neochonetes* (*Nongtaia*) subgen. nov.

Type species. *Neochonetes* (*Nongtaia*) *taoni* sp. nov.

Etymology. Derived from the name of Khao Nong Ta On.

Diagnosis. Similar to *Neochonetes* (*Neochonetes*) but shells small, subquadrate, with relatively narrow, distinct sulcus, distinct dorsal fold, distinct ornament of coarse capillae increasing in number by bifurcation.

Khao Nong Ta On	Khao Sam Ngan	Khao Bat Kwang
<i>Orthotichia waterhousei</i>	<i>Orthotichia waterhousei</i>	--
orthotetid fragments	--	orthotetid fragments
<i>Waterhouseiella speciosa</i>	<i>Waterhouseiella speciosa</i>	--
<i>Neochonetes</i> (<i>Nongtaia</i>) <i>taoni</i>	--	--
<i>Quinquenella?</i> sp.	--	--
--	<i>Marginifera otaria</i>	--
--	spinose productid	--
--	<i>Cleiothyridina seriata</i>	--
--	--	<i>Trigonotreta</i> sp.
<i>Spiriferellina adunctata</i>	<i>Spiriferellina adunctata</i>	--
<i>Hustedia ratburiensis</i>	--	--
--	<i>Notothyris triplax</i>	--

Table 2. Brachiopods from Khao Nong Ta On, Khao Sam Ngan and Khao Bat Kwang.

Discussion. The genus *Neochonetes* was discussed by Archbold (1981b: 111, 113) in terms of species composition and related species groups or stocks. One distinctive stock of mainly large species of Permian age was given the subgeneric name of *Sommeriella* Archbold (1982: 10) and the subgenus was widely indicated to be present throughout the Cimmerian Province, as tabulated by Archbold (1983) and listed for Western Australia by Archbold (1998b). Angiolini (1996) has added significantly to the knowledge of the mid-Permian species from the Karakorum.

The new material from Peninsular Thailand provides additional data on trends in the evolution of the *Neochonetes* group from the mid-Permian. Small species with distinct ornament, a subquadrate outline, a distinct and normally narrow ventral sulcus and corresponding dorsal fold appear in the Ufimian and Kazanian. In addition to the type species of *Neochonetes* (*Nongtaia*), the species *Chonetes pinegensis* Kulikov (1974) from the Kazanian of the Pinega River, Russia (see also Likharev 1931: pl. 1, figs 15, 16; pl. 3, fig. 14, identified as *Chonetes carbonifera* Keyserling) and *Neochonetes* cf. *pinegensis* of Stepanov et al. (1975: pl. 1, figs 3, 4) from the Kazanian of the Kanin Peninsula are assigned to the new subgenus. The *Chonetes* sp. (Likharev 1913: pl. 3, figs 17a, 17b) from the Kazanian of the region of Novgorod, Russia, is also allied.

Other species tentatively assigned to *Neochonetes* (*Nongtaia*) include the Kazanian (Murgabian) species *Chonetes arabicus* (Hudson & Sudbury 1959: 26, pl. 3, figs 6–16; pl. 6, figs 14–18; see also Archbold & Burrett 1990: fig. 1A–C) from Oman and *Neochonetes asseretoi* Fantini Sestini (1964) from Iran, both on the basis of their small size, subquadrate outlines and distinct external ornament and ventral sulci. The relatively small species *N. (Sommeriella) hardmani* Archbold (1993) from the Late Permian (Dzhulfian) of Western Australia is also allied to species of *Neochonetes* (*Nongtaia*), but possesses a somewhat broader sulcus. It is provisionally transferred to the new subgenus.

Neochonetes (*Nongtaia*) *taoni* sp. nov.

Fig. 3A–O

Neochonetes sp. Archbold, in Baird et al. 1993: 245.
Neochonetes (*Chonitella*) (sic), Baird et al. 1993: 247.

Holotype. NMV P120374, a complete dorsal valve from Khao Nong Ta On.

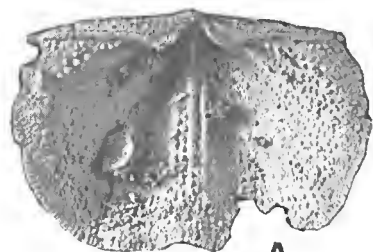
Paratypes. NMV P120375–NMV P120385, five ventral valves, one conjoined shell and five dorsal valves all from Khao, Nong Ta On.

Size ranges. Maximum width 6.1–13.2 mm; hinge width 6.1–11.5 mm; height of ventral valve 3.5–8.6 mm; height of dorsal valve 5.8–9.0 mm.

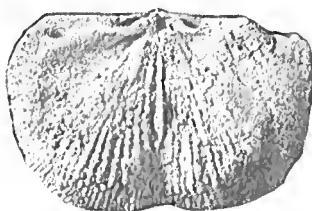
Description. Moderate sized *Neochonetes* (*Nongtaia*). Ventral valve convex with distinct sulcus arising within one millimetre of umbo. Central valley of sulcus narrow anteriorly. Dorsal valve gently concave with distinct but low median fold. Greatest width of shell at about mid-length; at or close to hinge line in juvenile specimens. Exterior shell surface with relatively coarse capillae increasing in number anteriorly by bifurcation and occasional pronounced growth lines, the latter particularly at the anterior of mature shells. Ventral interarea low, dorsal interarea very low. Ventral umbo low, cardinal spines project at about 40° close to umbo, at low angle (about 25°) at extremities of hinge line. Teeth distinct, moderately thickened. Delthyrium distinct. Prominent ventral median septum arises under delthyrium, extends anteriorly for up to two-thirds of valve length. Muscle scars weakly impressed. Parallel vascular trunks developed in mature ventral valves. Anterior and lateral margins of mature ventral valve strongly papillose.

Cardinal process low, distinctly bilobed on interior face, weakly quadrilobed on exterior face. Prominent, small, deep alveolus at base of process. Socket ridges prominent, thickened; sockets deep, wide. Lateral septa distinct at maturity. Median septum arises close to alveolus, thickened at maturity, raised anteriorly, extends anteriorly up to two-thirds valve length. Brachial ridges distinct at maturity; develop and enlarge from radial rows of

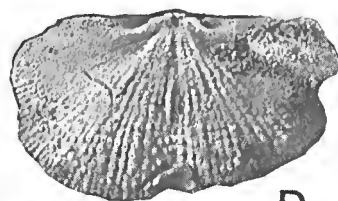
Fig. 3. A–O, *Neochonetes* (*Nongtaia*) *taoni* sp. nov. A, NMV P120375, ventral valve, interior view, $\times 4.5$. B, C, NMV P120376, dorsal valve, interior and exterior views, $\times 4.0$. D, NMV P120377, dorsal valve, interior view, $\times 4.5$. E, NMV P120378, ventral valve, interior view, $\times 8$. F, NMV P120379, dorsal valve, interior and exterior views, $\times 4.5$. G, H, Holotype, NMV P120374, dorsal valve, interior and exterior views, $\times 4.5$. I, J, NMV P120380, ventral valve, exterior and interior views, $\times 4.5$. K, NMV P120381, ventral valve, interior view, $\times 4.5$. L, NMV P120382, shell, ventral view, $\times 4.5$. M, NMV P120383, shell, ventral view, $\times 3.5$. N, NMV P120384, dorsal valve, interior view, $\times 3.5$. O, NMV P120385, dorsal valve, interior view, $\times 4.0$. All from Khao Nong Ta On.



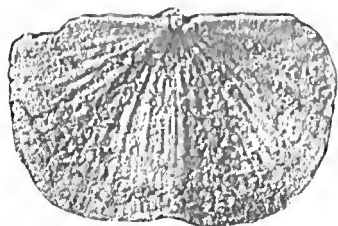
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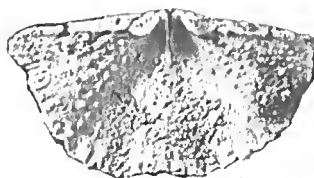
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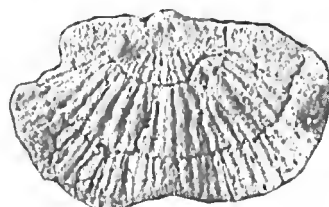
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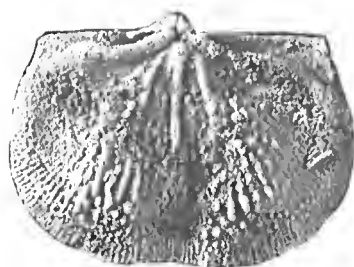
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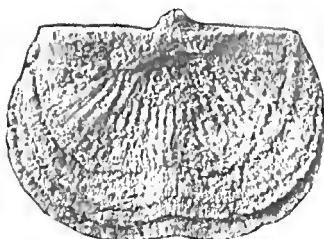
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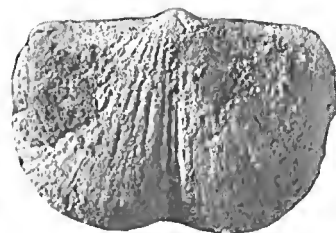
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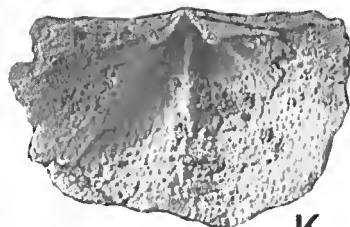
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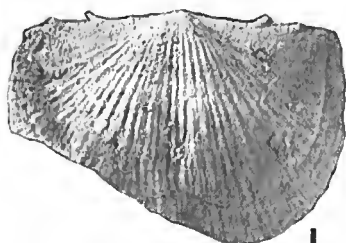
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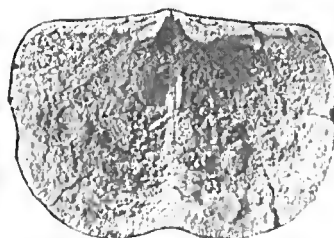
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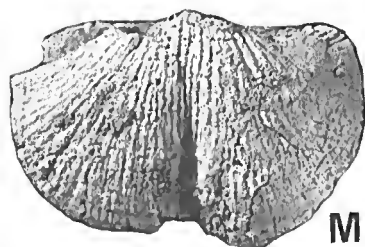
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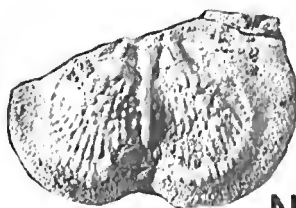
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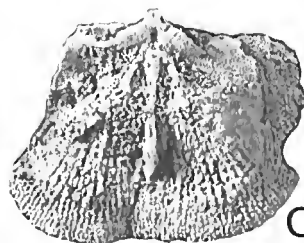
J



M



N



O

papillae. Anterior and lateral margins of dorsal valve interior with radiating rows of fine papillae. Posterior margins of dorsal valve interior smooth.

Discussion. *Neochonetes* (*Nongtaia*) *taoni* is readily distinguished from other species discussed above that are assigned to the new subgenus by means of its distinctive deep central valley normally developed in the sulcus. *N. (Nongtaia) urabicus* (Hudson & Sudbury, 1959) has less strongly developed internal features than the Thai species. The internal features of other related species from Northern European Russia are poorly known. The narrow sulcus of the new species is similar to that shown by several specimens of *Neochonetes* (*Sonneriella*) *irianeusis* Archbold (1992: fig. 2K-L, O-P) from the Artinskian of Irian Jaya, which may represent an ancestral species to the new subgenus.

Subgenus *Neochonetes* (*Zechiella*) subgen. nov.

Type species. *Chonetes davidsoni* von Schaubroth (1856: 222, pl. 11, figs 1a-b) from the Mergelschiefer near Ilmenau, Germany.

Etymology. Derived from the name Zechstein.

Diagnosis. Small, thin shelled *Neochonetes* with obsolescent radial capillae, sulcus absent, internal structures poorly developed.

Discussion. *Neochonetes* (*Zechiella*) consists of a distinctive group of upper Permian species from the Zechstein Basin and possibly Armenia as discussed briefly by Archbold (1981b: 113). With the formal naming of the subgenus *N. (Nongtaia)* it is also appropriate to name this second identifiable group of distinctive Upper Permian *Neochonetes*. Species assigned to *N. (Zechiella)* are the type species (see also Davidson 1880: 244, pl. 30, figs 1-2; Muir-Wood 1962: pl. 5, figs 28-29), *Chonetes woolacoti* Trechmann (1945: 346, pl. 15, figs 1-5b; see also Malzahn 1957: 99, pl. 10, figs 1-4) and *Chonetes kirkbyi* Trechmann (1945: 348, pl. 15, figs 6-9; see also Malzahn 1957: 102,

pl. 10, figs 5-6; pl. 11, fig. 3), all from both the English and German Zechstein. An allied species from the Kazanian of Armenia, with poorly developed radial ornament and no development of the ventral sulcus is *Neochonetes armenicus* Sokolskaya (1965: 209, pl. 32, figs 1-3, in Ruzhentsev & Sarycheva 1965), a species with clearly demarcated, flattened posterior lateral valve flanks.

Subfamily QUINQUENELLINAE Archbold, 1981c

Genus *Quinquenella* Waterhouse, 1975

Type species. *Quinquenella glabra* Waterhouse, 1975, from the Djhulfian of northwest Nepal.

Quinquenella? sp.

Fig. 4M

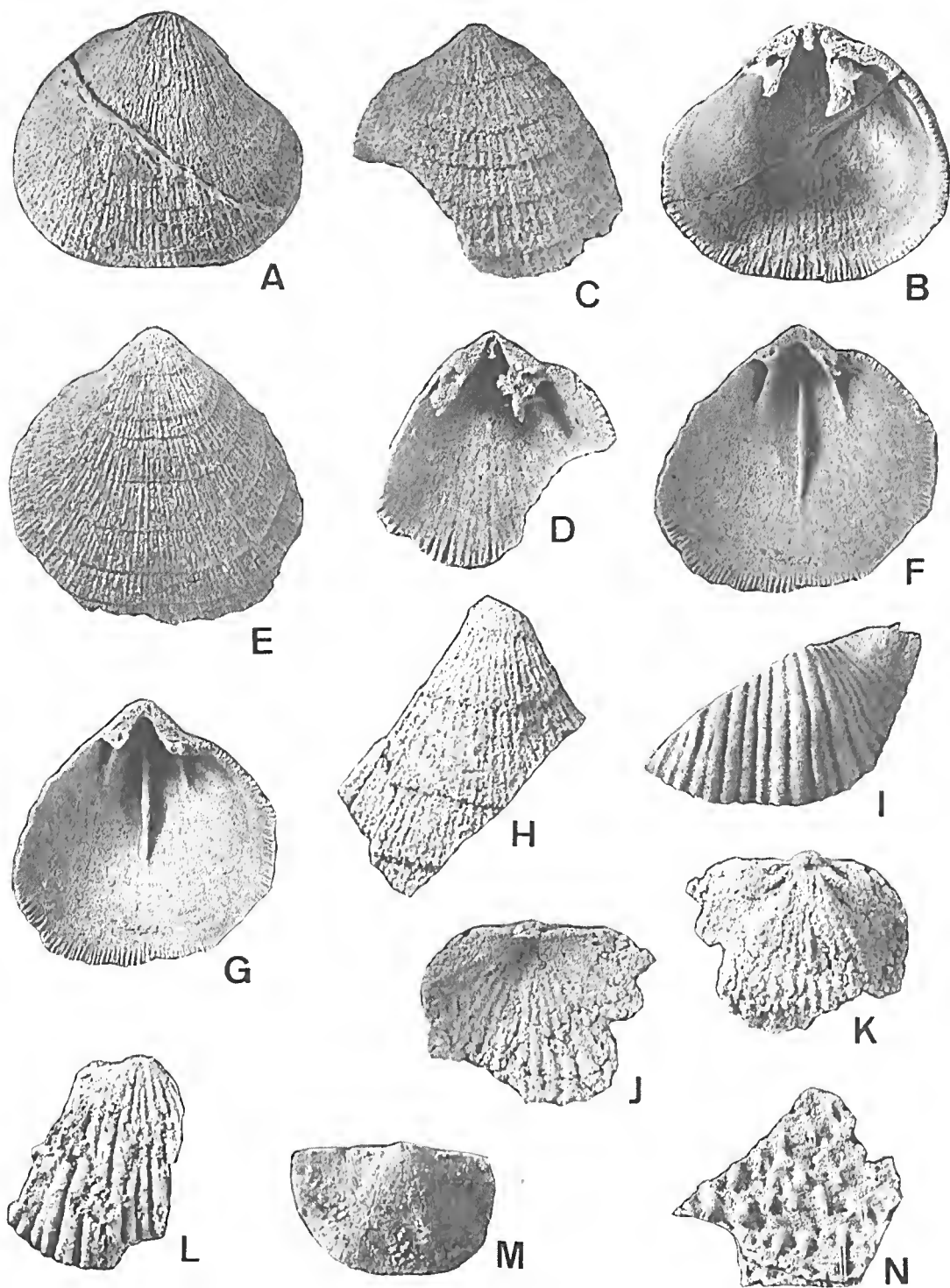
Material. A single juvenile ventral valve, NMV P120392, from the locality Khao Nong Ta On. The specimen is 5.0 mm wide and 3.5 mm in length.

Discussion. Chonetoids lacking radial ornament are rare in the Permian of Peninsular Thailand, being restricted to *Costachonetina* Waterhouse (1981a), *Demonedys* Grant (1976) and *Toruquistia* Paetzelmann (1930) from the Rat Buri Limestone and *Demonedys* (assigned to *Toruquistia* by Waterhouse 1981a) from the Ko Yao Noi Formation of the Kaeng Krachan Group.

The single available specimen of *Quinquenella?* sp. cannot be assigned to any of the above genera in view of its flattened median portion of the ventral valve and its more semicircular outline. The outline of the specimen is closest to that of Thai specimens of *Toruquistia* (Grant 1976: pl. 14, figs 1-10) but the latter do not possess a flattened median portion of the ventral valve.

Assignment of the specimen to *Quinquenella* can only be provisional due to the lack of information concerning the dorsal valve, however the genus is

Fig. 4. A-H, *Orthotichia waterhousei* Grant. A, B, NMV P120386, dorsal valve, exterior and interior views, $\times 4.5$. C, D, NMV P120387, dorsal valve, exterior and interior views, $\times 4.5$. E, G, NMV P120388, ventral valve, exterior, interior and tilted interior views, $\times 4.5$. H, NMV P120389, fragment of ventral valve, exterior view, $\times 4.5$. I-L, *Waterhouseiella speciosa* (Waterhouse & Piyasin). I, NMV P120409, incomplete shell, ventral view, $\times 4.5$. J, K, NMV P120390, dorsal valve, exterior and interior views, $\times 4.5$. L, NMV P120391, incomplete shell, ventral view, $\times 4.5$. M, *Quinquenella?* sp., NMV P120392, ventral valve, exterior view, $\times 6.5$. N, productid fragment, NMV P120393, exterior view, $\times 4.5$. H, J-L, N, from Khao Sam Ngan, remainder from Khao Nong Ta On.



known to occur from strata now considered to be of Kungurian age of Western Australia (Archbold 1981c) and Kungurian or probably Ufimian age of Irian Jaya (Archbold 1981d). The type species of *Quinquenella* is of Djulfian (=Wuchiapingian) age from Nepal. All species assigned to *Quinquenella* possess very similar ventral valve morphology. The specimens assigned to *Micraphelia*? sp. by Ishii et al. (1972: 68, pl. 1, figs 2, 4–8) from the Upper Permian of Perlis, Malaysia, may be allied judging from the outlines of the specimens but dorsal internal details are lacking.

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SPIRIFEROIDEA Waagen, 1883

Family SPIRIFERIDAE King, 1846

Subfamily TRIGONOTRETINAE Schuchert, 1893

Genus *Trigonotreta* Koenig, 1825

Type species. Trigonotreta stokesii Koenig, 1825, from the Sakmarian of Tasmania.

Trigonotreta sp.

Fig. 51–N

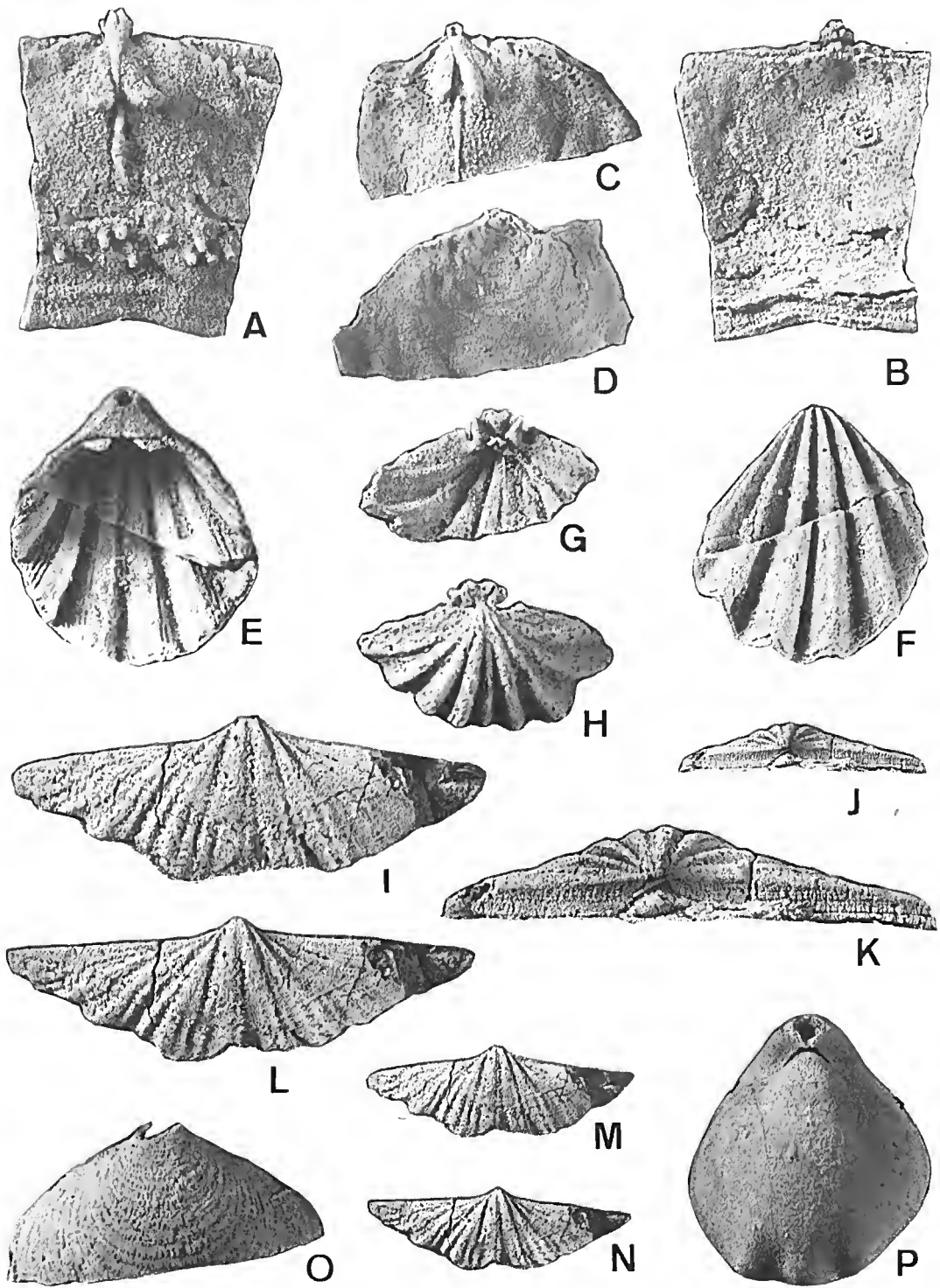
Material. A single juvenile ventral valve, NMV P120398, from Khao Bat Kwang. The specimen is 38 mm wide and 12 mm in length.

Discussion. Apart from the mention of my provisional identification of *Trigonotreta* by Baird et al. (1993: 247) the generic name has not been applied previously to any species from Peninsular Thailand. Grant (1976: 213, pl. 60, figs 43–44) recorded a single dorsal valve fragment of *Neospirifer* Fredericks (1923) from the

Rat Buri Limestone and Waterhouse (1981: 101, pl. 25, figs 3–5; pl. 26, figs 1–7) described a suite of specimens as *Neospirifer sterlitamakensis* (Gerasimov 1929) from Ko Yao Noi. Garson et al. (1975: pl. 3, figs 6, 10) had previously figured three mature specimens of *Neospirifer* that the present author has assigned to the subgenus *Neospirifer* (*Quadrosira*) (Archbold 1997: 214). The material described by Waterhouse (1981a) appears to fall into two groups—a true *Neospirifer* with fine, equidimensional costae (Waterhouse 1981: pl. 26, fig. 7) and a species with distinctive groups of three unequal costae and prominent, projecting growth lines as in a group of *Trigonotreta* species described from Tastubian to Ufimian strata of Western Australia (Archbold & Thomas 1986). All the Western Australia species possess relatively transverse juvenile stages of growth and hence are comparable with the new specimen, which is abraded and incomplete anteriorly. This group of *Trigonotreta* species is also known widely from peripheral Gondwanan regions such as Oman (Angiolini et al. 1997: fig. 15–12) and the Baoshan block, Yunnan (Shi et al. 1995: fig. 3–14; Shi et al. 1996: fig. 5c) from faunas of a Sakmarian age. True *Neospirifer sterlitamakensis* (Gerasimov 1929: 810, pl. 2, fig. 2) possesses fine, equidimensional costae and is better placed in *Neospirifer* as also shown by the specimen figured as *Spirifer fasciger* by Chernyshev (1902: 143, pl. 49, fig. 1a–b) and the specimen figured as *Spirifer striatus* var. *attenuatus* by Meller (1862: 66, pl. 2, fig. 4a–b) both assigned by Gerasimov to his new ‘mutation’. The species was treated as a variety by Stepanov (1948: 41, pl. 7, fig. 12) who figured a well preserved juvenile shell from the Gzhelian of Bashkiria. Mironova (1967: 43, pl. 4, fig. 6) also figured a well preserved small ventral valve from the same region and noted that *Neospirifer sterlitamakensis* ranged from the Gzhelian to the Sterlitamakian inclusive.

The presence of a specimen of *Trigonotreta* at Khao Bat Kwang may indicate that the assemblage is slightly older than that of the other two localities discussed in this study.

Fig. 5. A–D, *Marginifera otaria* Grant. A, B, NMV P120394, incomplete dorsal valve, interior and exterior views, $\times 5.0$. C, D, NMV P120395, incomplete dorsal valve, interior and exterior views, $\times 4.5$. E–H, *Hustedia ratburiensis* Waterhouse & Piyasin. E, F, NMV P120396, ventral valve, interior and exterior views, $\times 4.5$. G, H, NMV P120397, dorsal valve posterior portion, interior and exterior views, $\times 5.5$. I–N, *Trigonotreta* sp., NMV P120398, juvenile ventral valve, exterior, tilted exterior and interarea views, $\times 1$ and $\times 2$. O, *Cleiothyridina seriata* Grant, NMV P120399, ventral valve, exterior view, $\times 5.0$. P, *Notothyris triplax* Grant, NMV P120400, shell, dorsal view, $\times 4.5$. A–D, O, P, from Khao Sam Ngan; E–H, from Khao Nong Ta On; I–N, from Khao Bat Kwang.



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REFERENCES

- ALTERMANN, W., 1986. The upper Paleozoic pebbly mudstone facies of Peninsular Thailand and Western Malaysia—continental margin deposits of Paleocurasia. *Geologische Rundschau* 75: 371–381.
- ANGIOLINI, L., 1996. Permian brachiopods from Karakorum (Pakistan). Pt 2. *Rivista Italiana di Paleontologia e Stratigrafia* 102: 3–26.
- ANGIOLINI, L., BUCHER, H., PILLEVUIT, A., PLATEL, J.-P., ROGER, J., BROUTIN, J., BAUD, A., MARCOUX, J. & AL HASHMI, H., 1997. Early Permian (Sakmarian) brachiopods from Southeastern Oman. *Geobios* 30: 379–405.
- ANGIOLINI, L., NICORA, A., BUCHER, H., VACHARD, D., PILLEVUIT, A., PLATEL, J.-P., ROGER, J., BAUD, A., BROUTIN, J., AL HASHMI, H. & MARCOUX, J., 1998. Evidence of a Guadalupian age for the Khuff Formation of Southeastern Oman: Preliminary report. *Rivista Italiana di Paleontologia e Stratigrafia* 104: 329–340.
- ARCHBOLD, N. W., 1981a. Permian brachiopods from Western Irian Jaya, Indonesia. *Geological Research and Development Centre, Paleontology Series* 2: 1–25.
- ARCHBOLD, N. W., 1981b. Studies on Western Australian Permian brachiopods 2. The family Rugosochonetidae Muir-Wood 1962. *Proceedings of the Royal Society of Victoria* 93: 109–128.
- ARCHBOLD, N. W., 1981c. *Quinquenella* (Chonetidina, Brachiopoda) from the Permian of Western Australia. *Journal of Paleontology* 55: 204–210.
- ARCHBOLD, N. W., 1981d. *Quinquenella magnifica* sp. nov. (Chonetidina, Brachiopoda) from the Permian of Irian Jaya, Indonesia: a study of the ontogeny of a chonetid brachiopod. *Geological Research and Development Centre, Paleontology Series* 2: 27–34.
- ARCHBOLD, N. W., 1982. *Sommeriella*, a new name for the Permian chonetacean brachiopod subgenus *Sommeria* Archbold 1981. *Proceedings of the Royal Society of Victoria* 94: 10.
- ARCHBOLD, N. W., 1983. Permian marine invertebrate provinces of the Gondwanan Realm. *Alcheringa* 7: 59–73.
- ARCHBOLD, N. W., 1992. Early Permian Brachiopoda from Irian Jaya. *BMR Journal of Australian Geology and Geophysics* 12: 287–296.
- ARCHBOLD, N. W., 1993. Studies on Western Australian Permian brachiopods 11. New genera, species and records. *Proceedings of the Royal Society of Victoria* 105: 1–29.
- ARCHBOLD, N. W., 1997. Studies on Western Australian Permian brachiopods 14. The fauna of the Artinskian High Cliff Sandstone, Perth Basin. *Proceedings of the Royal Society of Victoria* 109: 199–231.
- ARCHBOLD, N. W., 1998a. Marine biostratigraphy and correlation of the West Australian Permian Basins. In *The Sedimentary Basins of Western Australia* 2, P. G. Purcell & R. R. Purcell, eds, Petroleum Exploration Society of Australia Limited, Perth, 141–151.
- ARCHBOLD, N. W., 1998b. Correlations of the Western Australian Permian and Permian ocean circulation patterns. *Proceedings of the Royal Society of Victoria* 110: 85–106.
- ARCHBOLD, N. W. & BURRETT, C. F., 1990. Re-assessment of the Arabian Permian chonetid brachiopod *Chonetes arabicus* Hudson & Sudbury. *Proceedings of the Royal Society of Victoria* 102: 121–122.
- ARCHBOLD, N. W., PIGRAM, C. J., RATMAN, N. & HAKIM, S., 1982. Indonesian Permian brachiopod fauna and Gondwana–South-East Asia relationships. *Nature* 296: 556–558.
- ARCHBOLD, N. W., SHAH, S. C. & DICKINS, J. M., 1996. Early Permian brachiopod faunas from Peninsular India: Their Gondwana relationships. *Historical Biology* 11: 125–135.
- ARCHBOLD, N. W. & SHU, G. R., 1995. Permian brachiopod faunas of Western Australia: Gondwanan–Asian relationships and Permian climate. *Journal of Southeast Asian Earth Sciences* 11: 207–215.

Fig. 6. A–M, *Spiriferellina adunctata* Waterhouse & Piyasin. A, B, NMV P120401, ventral valve, posterior and ventral views, $\times 4.5$. C, D, NMV P120402, incomplete shell, anterior and dorsal views, $\times 4.5$. E, F, NMV P120403, dorsal valve, interior and exterior views, $\times 5.0$. G, H, NMV P120404, dorsal valve, exterior and interior views, $\times 5.0$. I, NMV P120405, dorsal valve, interior view, $\times 5.0$. J, NMV P120406, ventral valve, exterior view, $\times 7.0$. K, NMV P120407, ventral valve, exterior view, $\times 5.0$. L, M, NMV P120408, tilted interior view and interior view, $\times 5.0$. I, J, from Khao San Ngan, remainder from Khao Nong Ta On.

- ARCHBOLD, N. W. & THOMAS, G. A., 1986. *Neospirifer* and *Trigonotreta* (Spiriferida, Brachiopoda) from the Permian of Western Australia. *Alcheringa* 10: 125–161.
- BAIRD, A. & BOSENCE, D., 1993. The sedimentological and diagenetic evolution of the Ratburi Limestone, Peninsular Thailand. *Journal of Southeast Asian Earth Sciences* 8: 173–180.
- BAIRD, A., DAWSON, O. & VACHIARD, D., 1993. New data on biostratigraphy of the Permian Ratburi Limestone from north Peninsular Thailand. In *International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies & Palaeontology*, T. Thanasuthipitak, ed., Chiang Mai University, Chiang Mai, Vol. 2: 243–259.
- BRIGGS, D. J. C., 1998. Permian Productidina and Strophalosiidina from the Sydney–Bowen Basin and New England Orogen: systematics and biostratigraphic significance. *Memoir of the Association of Australasian Palaeontologists* 19: 1–258.
- BROWN, G. F., BURAVAS, S., CHARALJAVANAPHET, J., JALICHANDRA, N., JOHNSTON, W. D. JNR, SRESTHAPUTRA, V. & TAYLOR, G. C. JNR, 1951. Geologic reconnaissance of the mineral deposits of Thailand. *United States Geological Survey Bulletin* 984: 1–183.
- BUNOPAS, S., 1976. On the stratigraphic successions in Thailand—a preliminary summary. *Journal of the Geological Society of Thailand* 2: 31–58.
- CHERNYSHEV, F. N. (TSCHERNYSCHIEV, T. N.), 1902. Verkhnekamennougol'nye brachiopody Urala i Timana. *Trudy Geologicheskogo Komiteta* 16(2): 1–749 + Atlas 63 pls.
- DAVIDSON, T., 1880. A monograph of the British Fossil Brachiopoda. Vol. IV., Pt 3. Supplement to the Permian and Carboniferous species. *Palaeontographical Society Monograph* 34: 243–315, pls 30–37.
- DAWSON, O., RACEY, A. & WHITTAKER, J. E., 1993. The palaeoecological and palaeobiogeographic significance of *Shanila* (Formanifera) and associated foraminifera/algae from the Permian of peninsula Thailand. In *International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies & Palaeontology*, T. Thanasuthipitak, ed., Chiang Mai University, Chiang Mai, Vol. 2: 283–298.
- FANTINI SESTINI, N., 1964. Diagnosi di forme nuove. *Neochonetes asseretoi* sp. n. *Rivista Italiana di Paleontologia e Stratigrafia* 70: 899.
- FANG, R.-S., 1994. The discovery of cold-water brachiopod *Stepanoviella* fauna in Baoshan region and its geological significance. *Yunnan Geology* 13: 264–277.
- FONTAINE, H., CHONGLAKMANI, C., BIN AMNAN, I. & PIYASIN, S., 1994a. A well-defined Permian biogeographic unit: Peninsular Thailand and northwest Peninsular Malaysia. *Journal of Southeast Asian Earth Sciences* 9: 129–151.
- FONTAINE, H., SATTAYARAK, N. & SUTEETHORN, V., 1994b. Permian corals of Thailand. *CCOP Technical Bulletin* 24: i–vi, 1–171.
- FREDERICKS, G. N., 1923. –Teoreticheskie issledovaniya v oblasti voprosov sistematiki–. In: *Otchet o sostoyanii i deyatelnosti Geologicheskogo Komiteta v 1919 gody. Izvestiya Geologicheskogo Komiteta* 39(2): 313–316.
- GARSON, M. S., YOUNG, B., MITCHELL, A. H. G. & TAIT, B. A. R., 1975. The geology of the tin belt in Peninsular Thailand around Phuket, Phangnga and Takua Pa. *Institute of Geological Sciences. Overseas Memoir* 1: i–xii, 1–122, 10 pls, 9 maps.
- GERASIMOV, N. P., 1929. Brachiopody Sterlitinskogo Izvestnyaya. *Uchenye Zapiski Kazanskogo Gosudarstvennogo Universiteta imeni V.I. Ul'yanova-Lenina, Otdel Estestvenno-Istoricheskikh Nauk* 89: 779–872, pls 1–4.
- GRANT, R. E., 1976. Permian brachiopods from Southern Thailand. *Journal of Paleontology* 50(3) supplement (*Paleontological Society Memoir*) 9: 1–269.
- HAMADA, T., 1960. Some Permo–Carboniferous fossils from Thailand. *Scientific papers of the College of General Education University of Tokyo* 10: 337–360, pls 1–2.
- HUDSON, R. G. S. & SUDBURY, M., 1959. Permian Brachiopoda from South-East Arabia. *Notes et Memoires sur le Moyen-Orient* 7: 19–55, pls 1–6.
- INGAVAT-HELMCKE, R. & HELMCKE, D., 1994. Permian facies—realms in Thailand. In *Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia*, P. Angsuwathana, T. Wongwanich, W. Tansathien, S. Wongsomak & J. Tulyatid, eds, Department of Mineral Resources, Bangkok, 100–105.
- IQBAL, N., BROUTIN, J., IZART, A., COQUEL, R., VACHIARD, D. & HASAN BAQRI, S. R., 1998. Quelques donnees stratigraphiques sure le Permien inferieur du Salt Range (Pakistan). *Geodiversitas* 20: 724–730.
- ISHII, K.-I., KATO, M., NAKAMURA, K. & NOGAMI, Y., 1972. Permian brachiopods from Bukit Tungku Lembu, Perlis, Malaysia. *Journal of Geosciences, Osaka City University* 15: 65–77.
- KOENIG, C., 1825. *Icones Fossilium Sectiles*. London. 4 pp., 19 pls.
- KULIKOV, M. V., 1974. O rasslenii i usloviyakh obitaniya fauny v severnoi chasti Kazanskogo Morya. *Trudy Vsesoyuznogo ordena Lenina Nauchno-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI), Novaya Seriya* 182: 138–153.
- LIKHAREV, B. K. (LICHAREW, B. K.), 1913. Fauna Permskikh' Otlozhenii Okrestnostei Goroda Kirillova Novgorodskoi Gubernii. *Trudy Geologicheskogo Komiteta, Novaya Seriya* 85: 1–99, pls 1–5.
- LIKHAREV, B. K. (LICHAREW, B. K.), 1931. Materialy k poznaniyu fauny Verkhne-Permskikh otlozhenii Severnogo Kraya. *Trudy Glavnogo Geolog-Razvedochnogo Upravleniya V.S.N.Kh., S.S.S.R. Vypusk* 71: 1–42, pls 1–3.
- MAIZAHN, E., 1957. Neue fossilfunde und vertikale verbreitung der niedertheinischen Zechsteinfauna in den Bahrungen Kamp 4 und Friedrich Heinrich 57 bei Kamp-Lintfort. *Geologische Jahrbuch* 73: 91–126.

- MANTAJIT, N., 1978. A note on the Permo-Carboniferous stratigraphic succession in Thailand. In *Proceedings of the Third Regional Conference on Geology and Mineral Resources of Southeast Asia*, P. Nutalay, ed., Asian Institute of Technology, Bangkok, 851.
- MANTAJIT, N., 1999. Thailand and Tethys Sea. In *Shallow Tethys 5*, B. Ratanasthien & S. L. Ricb, eds, Chiang Mai University, Chiang Mai, ix-xxvii.
- MELLER, V. I. (also MOELLER, V. I. and MÖLLER, V. I.), 1862. Geologicheskaya i paleontologicheskaya zametki ob' osadkakh gornoizvestkovoi formatsii otklonov' khrebtu Ural'skago. *Gornyi Zhurnal* 1862, chast'4, 10/11: 43-81, 163-208, pls 1-10.
- METCALFE, I., 1985. Stratigraphy, palaeontology and palaeogeography of the Carboniferous of southeast Asia. *Societe Geologique de France, Memoire* 147: 107-118.
- METCALFE, I., 1990. Allochthonous terrane processes in southeast Asia. *Philosophical Transactions of the Royal Society, London A331*: 625-640.
- METCALFE, I., 1993. Southeast Asian Terranes: Gondwanaland origins and evolution. In *Gondwana Eight. Assembly, Evolution and Dispersal*, R. H. Findlay, R. Unrug, M. R. Banks & J. J. Veivers, eds, A. A. Balkema, Rotterdam, 181-200.
- METCALFE, I., 1995. Gondwana dispersion and Asian accretion. *Geological Survey of Vietnam, Journal of Geology, Series B* 5-6: 223-266.
- MIRONOVA, M. G., 1967. *Pozdnekamennougol'nye Brachiopody Bashkirii*. Leningradskii Gosudarstvennyi Universitet, Leningrad, 1-62, 5 pls.
- MITCHELL, A. H. G., YOUNG, B. & JANTARAPIPA, W., 1970. The Phuket Group, Peninsular Thailand, a Palaeozoic? geosynclinal deposit. *Geological Magazine* 107: 411-428.
- MUIR-WOOD, H. M., 1962. *On the morphology and classification of the brachiopod suborder Chonetoida*. British Museum (Natural History), London, i-viii, 1-132, pls 1-16.
- PAECKELMANN, W., 1930. Die Brachiopoden des Deutschen Unter carbons, I. *Abhandlungen der Preussischen geologischen Landesanstalt, Neue Folge* 122: 1-440, pls 1-16.
- PITAKPAIVAN, K. & MANTAJIT, N., 1981. Summary of Stratigraphy. *Geological Survey of Thailand Memoir* 4: 51-55.
- PIYASIN, S., 1975. Review of the Ratburi Group. In *Proceedings of the Conference on the Geology of Thailand*, R. B. Stokes, C. Tantisukrit & K. V. Campbell, eds, Chiang Mai University, Department of Geological Sciences, Chiang Mai, Special Publication 1, Vol. 1: 65-99.
- PIYASIN, S., 1976. Stratigraphy and sedimentology of the Kaeng Krachan Group (Carboniferous). In *Proceedings of the Conference on the Geology of Thailand*, R. B. Stokes & C. Tantisukrit, eds, Chiang Mai University, Chiang Mai, Department of Geological Sciences, Special Publication 1, Vol. 2: 25-35.
- RACEY, A., SMITH, A. B. & DAWSON, O., 1994. Permian echinoderms from Peninsula Thailand. In *Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia*, P. Angsuwathan, T. Wongwanich, W. Tansathien, S. Wongsomsak & J. Tulyatid, eds, Department of Mineral Resources, Bangkok, 106-114.
- RAKSASKULWONG, L. & WONGWANICH, T., 1993. *Stratigraphy of the Kaeng Krachan Group, Peninsular and Western Thailand*. Geological Survey of Thailand, Bangkok, 1-66.
- RAKSASKULWONG, L. & WONGWANICH, T., 1994. Stratigraphy of the Kaeng Krachan Group, Peninsular and Western Thailand. *Annual Report of the Geological Survey of Thailand* 1994: 106-116.
- RUZHIENTSEV, V. E. & SARYCHEVA, T. G., 1965. Razvitie i smena morskikh organizmov na rubezhe Palcozoia i Mezozoya. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta* 108: 1-432.
- SAWATA, H., ARPORNISUWAN, S. & PISUTHA-ARNOWD, V., 1975. Note on geology of Khao Phra, Phetchaburi, west Thailand. *Journal of the Geological Society of Thailand* 1: 31-49.
- SCHIAUROT, C. VON, 1856. Ein neuer Beitrag zur Palaontologie des deutschen Zechsteingebirges. *Zeitschrift der deutschen geologischen Gesellschaft* 8: 211-245, pl. 11.
- SHI, G. R. & ARCHIBOLD, N. W., 1995. Permian brachiopod faunal sequence of the Shan-Thai terrane/palaeoclimatic implications. *Journal of Southeast Asian Earth Sciences* 11: 177-187.
- SHI, G. R., ARCHIBOLD, N. W. & FANG, Z.-J., 1995. The biostratigraphical and palaeobiogeographical significance of an Early Permian brachiopod fauna from the Dingjiazhai Formation, Baoshan Block, Western Yunnan, China. *Geological Survey of Vietnam, Journal of Geology, Series B* 5-6: 63-74.
- SHI, G. R., FANG, Z.-J. & ARCHIBOLD, N. W., 1996. An early Permian brachiopod fauna of Gondwanan affinity from the Baoshan block, Western Yunnan, China. *Alcheringa* 20: 81-101.
- SHI, G. R., LEMAN, M. S. & TAN, B. K., 1997. Early Permian brachiopods from the Singa Formation of Langkawi Island, northwestern Peninsular Malaysia: biostratigraphical and biogeographical implications. In *Proceedings of the International Conference on Stratigraphy and Tectonic Evolution of Southeast Asia and the South Pacific*. Department of Mineral Resources, Bangkok, 62-72.
- STAUFFER, P. H., 1983. Unraveling the mosaic of Paleozoic crustal blocks in southeast Asia. *Geologische Rundschau* 72: 1061-1080.
- STAUFFER, P. H. & MANTAJIT, N., 1981. Late Palaeozoic tilloids of Malaya, Thailand and Burma. In *Earth's Pre-Pleistocene Glacial Record*, M. J. Hamhrey & W. B. Harland, eds, Cambridge University Press, Cambridge, 331-335.
- STEPANOV, D. L., 1948. Verkhnekamennougol'nye Brachiopody Bashkirii. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedoch-nogo Instituta (VNIGRI), Novaya Seriya* 22: 1-65, pls 1-11.

- STEPANOV, D. L., KULIKOV, M. V. & SULTANAEV, A. A., 1975. Stratigrafiya i brakhiopody Verkhneperm-skikh otlozhenii Poluostrova Kanin. *Vestnik Leningradskogo Universiteta* 6: 51-65.
- STOKES, R. B., 1975. Pre-Ratburi Group Paleozoic rocks. In *Proceedings of the Conference on the Geology of Thailand*, R. B. Stokes, C. Tantisukrit & K. V. Campbell, eds, Chiang Mai University, Department of Geological Sciences, Chiang Mai, Special Publication 1, Vol. 1: 21-64.
- TRECHMANN, C. T., 1945. On some new Permian fossils from the Magnesium Limestone near Sunderland. *Quarterly Journal of the Geological Society of London* 100: 333-354, pl. 15.
- WATERHOUSE, J. B., 1973. Permian brachiopod correlations for South-East Asia. *Bulletin of the Geological Society of Malaysia* 6: 187-210.
- WATERHOUSE, J. B., 1975. New Permian and Triassic brachiopod taxa. *Papers, Department of Geology, University of Queensland* 7(1): 1-23.
- WATERHOUSE, J. B., 1976. World correlations for Permian marine faunas. *Papers, Department of Geology, University of Queensland* 7(2): 1-232.
- WATERHOUSE, J. B., 1981a. Early Permian brachiopods from Ko Yao Noi and near Krabi, Southern Thailand. *Geological Survey of Thailand, Memoir* 4: 43-213, pls 1-34.
- WATERHOUSE, J. B., 1981b. Age of Rat Buri Limestone of Southern Thailand. *Geological Survey of Thailand, Memoir* 4: 1-42.
- WATERHOUSE, J. B., 1982. An early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine* 119: 337-354, pls 1-3.
- WATERHOUSE, J. B. & PIYASIN, S., 1970. Mid-Permian brachiopods from Khao Phrik, Thailand. *Palaeontographica, Abteilung A* 135: 83-197, pls 14-32.
- WEBSTER, G. D. & JELL, P. A., 1993. Early Permian inadunate crinoids from Thailand. *Memoirs of the Queensland Museum* 33: 349-359.
- YANAGIDA, J., 1971. Permian brachiopods from Khao Phrik, near Rat Buri, Thailand. *Geology and Palaeontology of Southeast Asia* 8: 69-96, pls 14-16.
- YANAGIDA, J., 1984. Carboniferous and Permian brachiopods of Thailand and Malaysia with a brief note on the Mesozoic. *Geology and Palaeontology of Southeast Asia* 25: 187-194.
- YOUNG, B. & JANTARANIPA, W., 1970. The discovery of Upper Palaeozoic fossils in the 'Phuket Series' of Peninsular Thailand. *Proceedings of the Geological Society of London* 1662: 5-7.

DISTRIBUTION AND CONSERVATION STATUS OF THE
STONEFLY *THAUMATOPERLA FLAVEOLA* BURNS & NEBOISS
IN THE MT BULLER-STIRLING AREA

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A total of 90 sites where sampling suitable for the detection of the stonefly *Thaumatoperla flaveola* Burns & Neboiss were identified. These sites occupied an area of about 30 km by 30 km around Mt Buller, including the upper reaches of the Deletite, Howqua and King River catchments. *T. flaveola* was located at only 28 sites in an area 12 km by 10 km, almost exclusively in the upper tributaries of the Deletite River above 1000 m ASL. Surveys at sites outside this restricted area consistently failed to locate the species, suggesting that the species has a restricted distribution based on the Mt Buller-Stirling massif.

Assigning a conservation status to the species, based on the criteria for conservation status defined by the International Union for Conservation of Nature & Natural Resources (IUCN) was relatively simple. Given the fragmented nature of the distribution, the low dispersal powers of the species and the proximity of threatening processes, the appropriate conservation status of *Thaumatoperla flaveola* is 'Endangered'.

THE stonefly family Eustheniidae (Insecta: Plecoptera) is considered to be of high scientific interest as it is believed to be the most archaic and least evolved group of stoneflies. Zwick (1979) quoted Tillyard (1921) as concluding that 'though existing today, they represent the original archtypic family of the Order, from which all other types must have been derived'. The subfamily Eustheniidae (comprising *Thaumatoperla* Tillyard and *Eusthenia* Gray in Australia) is found in Tasmania and the mainland, but 'does not extend far to the north on the mainland' and the two genera 'probably are ancient relics in Australia' (Zwick 1979).

Four species of *Thaumatoperla* (*T. flaveola* Burns & Neboiss, *T. alpina* Burns & Neboiss, *T. robusta* Tillyard and *T. timmsi* Zwick) are recognised from Australia, all from the Victorian high country. The four species are believed to have disjunct (allopatric) and relatively restricted distributions. *T. alpina* has previously been recorded only from streams on Mt Mackay, Mt Fainter and the Bogong High Plains, *T. timmsi* has only been found at a single location near Lake Tarli Kam and, prior to this study, *T. flaveola* has previously only been known from a few locations on Mt Stirling and Mt Buller. *T. robusta* has the widest known distribution, collected from isolated mountains from Mt Donna Buang to Mt Baw Baw.

Like many invertebrates associated with aquatic habitats, *Thaumatoperla* species have an aquatic larval stage restricted to freshwater systems. Most of the life cycle (up to a number of years) is passed as the immature freshwater stage. The terrestrial winged adult stage emerges from the stream following a final moult and is short lived (from a few days to a few months), but has extremely restricted powers of flight and dispersal (Pettigrove 1991).

As a result of the perceived limited distribution of each of the species, all four of the *Thaumatoperla* species are listed as threatened in Victoria, with *T. flaveola* listed as Vulnerable (CNR 1995). Two of the species (*T. flaveola* and *T. alpina*) are listed under Schedule 2 of the *Flora & Fauna Guarantee Act* 1988, requiring the Victorian Government to produce Action Statements outlining management measures to ensure their survival.

Because of the concerns about the potential impact of current and proposed alpine resort development and forestry and grazing activities in the Mt Stirling area on *Thaumatoperla flaveola*, all development in the area must take into account protection of streams for this species. Special forestry prescriptions are in force in the area, including wider than normal buffer strips left around the streams to prevent siltation.

Surveys for the species have been conducted sporadically over the past 10 years (eg. Pettigrove 1991). This paper summarises the results of those surveys, adding the results of a previously unpublished survey conducted by the Department of Natural Resources & Environment (NRE) in January 1994–April 1995, to conclusively determine the distribution and conservation status of the species.

SURVEY SITES

The Mt Buller–Stirling massif is drained by three major river systems; the wet-flowing Delatite and Howqua Rivers (both tributaries of the Goulburn River) and the north-flowing King River (which flows into the Ovens River at Wangarratta).

Historical data from 20 sites where *Thaumatoperla flaveola* were located was obtained from the Wildlife Atlas database held by the Flora & Fauna Branch of the NRE. An additional 31 sites where sampling suitable for *T. flaveola* was conducted were identified from published (Pettigrove 1991) and unpublished reports on original surveys (where full survey site data were included).

For the 1994–95 survey, 30 sites in all three catchments were selected from maps and local knowledge, based mainly on available access to streams. Where possible, a number of sites with a range of altitudes were located in each catchment and subcatchment. A number of these sites (6) were at locations where previous surveys had been conducted, meaning that data from a total of 75 sites were available from all sources.

SURVEY METHODS (1994–95)

For the surveys conducted during January 1994–April 1995, a total of one person hour was spent searching for *Thaumatoperla* nymphs at each site. This involved the collection of both kick samples which were placed in white trays and searched by hand, and by physically picking up likely habitat elements (stones and wood) and examining them by eye for larger specimens. Surrounding vegetation was also searched for adults (although none were found).

It is recognised that the species has been located buried quite deep in the bed of the stream, but no attempt was made to sample this hyporheic habitat. As the aim was to determine the distribution of the species, it was decided that a rapid wide ranging survey was more appropriate. The technique

employed has been successful in determining the distribution of another large threatened eustheniid stonefly (*Eusthenia nothofagi*) in the Otway Ranges (Doeg & Reed 1995) and successfully located *T. flaveola* at sites where it had previously been recorded.

IDENTIFICATION OF SPECIMENS

While it is possible to identify eustheniid stoneflies to the generic level in the field (ie. to distinguish between *Thaumatoperla* and *Eusthenia* individuals), there are no satisfactory characteristics by which the nymphs of each of the *Thaumatoperla* species can be distinguished.

Therefore, it can only be assumed that all individuals of *Thaumatoperla* collected and identified within the study area were, in fact, *T. flaveola*. This is based on the observation of Zwick (1979: 24) that 'as the species are allopatric, assignment of larvae to particular species is usually no problem'. Also, no adults of any other *Thaumatoperla* species have been collected from the Mt Buller–Stirling area during any previous survey.

RESULTS

From the 75 sites where data are available, *Thaumatoperla* nymphs have been located at 28 sites in the Mt Buller–Stirling area (Fig. 1). The majority of sites (18 sites) where the species was recorded lie within the upper Delatite River basin. There are relatively few sites (7 sites) within the upper Delatite River where the species has not been recorded at some time.

A further 6 sites were located in the upper tributaries of the Howqua River and 4 sites in the upper tributaries of the King River. These sites were invariably in the very uppermost tributaries draining just over the ridgeline from the Delatite basin. This is particularly evident at sites on the King River tributaries (top of Fig. 1), where the species was absent from numerous sites further downstream.

While many sites were sampled outside this area (25 sites are not shown in Fig. 1), no specimens of *Thaumatoperla* were recorded. The sites not shown included many on the opposite ridge on the Howqua River (around Rocky Knob) and surrounding catchments (Macalister, Wonnangatta, Buffalo and Dandongadale Rivers), mostly within 20–30 km of Mt Buller.

Assuming that all *Thaumatoperla* specimens collected were *T. flaveola*, it can therefore be stated with some certainty that the species is restricted to a small geographic area around Mt Buller, Mt Stirling and Mt Winstanley, either side of the ridgeline surrounding the headwaters of the Delatite River. The lowest altitude that the species was recorded at is 1100 m. As such, the area included in the distribution is approximately 12 km measured from east to west and 10 km north to south.

DISCUSSION

Distribution of Thaumatoperla flaveola

Accurately defining the distribution of any invertebrate species is difficult, especially if relying on historical information (eg. Wildlife Atlas data). In the main, historical data only includes sites where a particular species has been located, giving no information on areas where suitable searches have been conducted without locating the target

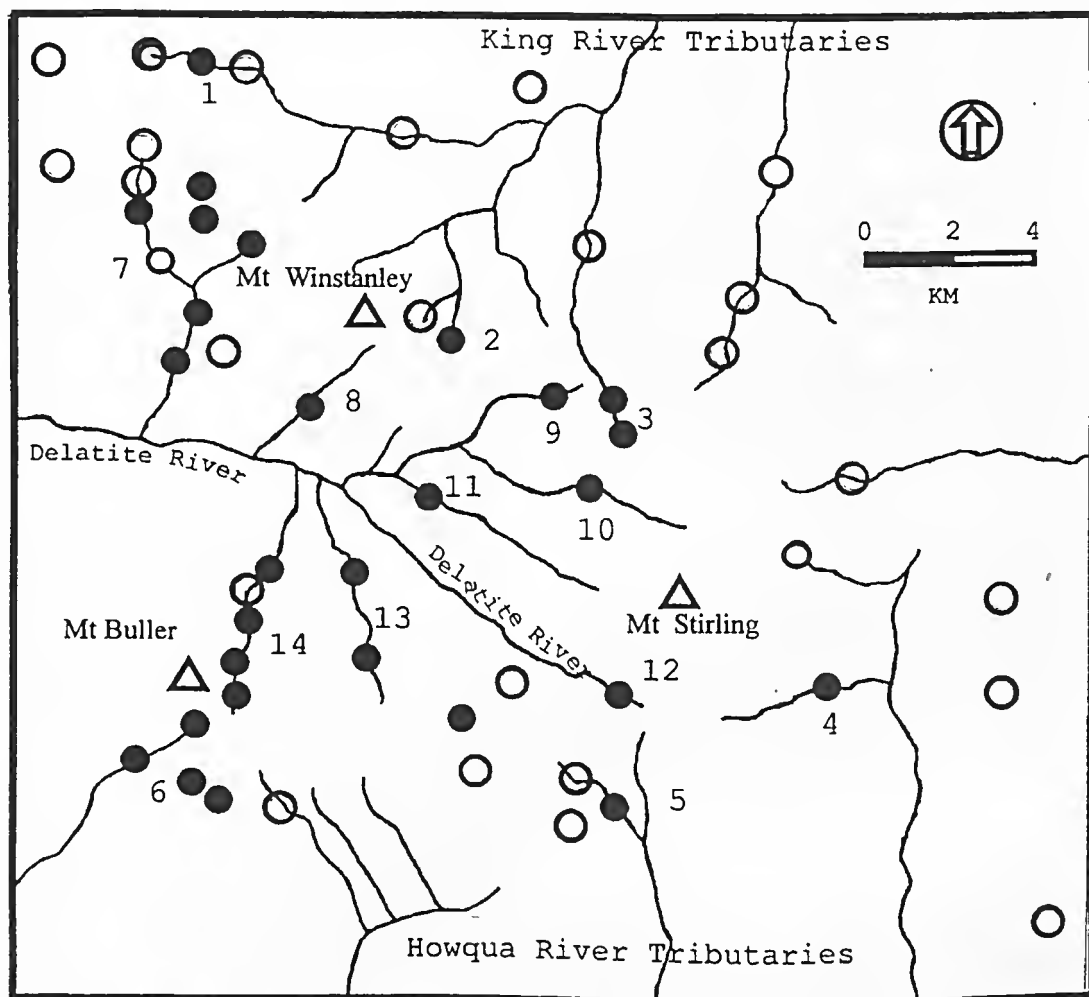


Fig. 1. Map of the Mt Buller-Mt Stirling area showing the location of sites where *Thaumatoperla flaveola* have been recorded (●) and not recorded despite suitable sampling (○). A further 25 sites where the species were not recorded are off the area of the map. Numbers refer to discrete locations discussed in the text.

species. Hence, while a distribution may be defined on the presence of the species, there are often no data to show the species to be absent outside this area.

This can result in misleading conclusions as to the true distribution of some species. For example, works like the Zoological Catalogue (eg. Commonwealth of Australia 1988) list many invertebrate species that have only been located at the type locality. Many other taxonomic works also only list a few sites where a species has been found. These suggest that the species have extremely limited distributions, which may not be true.

In this case, specific surveys and the interpretation of original data sets has allowed an accurate definition of the distribution of *Thaumatoperla flaveola* in the Mt Buller–Stirling area. The species was consistently recorded in a small area around Mt Buller, Mt Stirling and Mt Winstanley, in an area 12 km by 10 km. Searching at a large number of sites outside this area consistently failed to find the species. Rather than the sites where the species was located, it is the density of sites searched outside the known distribution, and the consistent failure to locate the species, that provides adequate evidence to delineate the true distribution.

The species has been recorded in a variety of stream types, ranging from small, almost dry tributaries to larger fast flowing streams. However, there are certain sites with comparatively high abundances, as occasionally noted during 1994–95 and other surveys. The most obvious such sites have been located in two tributaries of Currajong Creek and in Brown Creek (sites 7 and 8 in Fig. 1).

These sites had similar morphologies, where the stream was composed of a series of terraces, separated by steep sections. The flow was low and mainly percolated through the open stream bed. It may well be proven that these are the preferred habitats of the species, as fewer individuals have been located at sites with different morphologies. Further work needs to be done on the ecological requirements of the species before a preferred habitat or stream type can be positively identified.

Conservation status of Thaumatoperla flaveola

Data such as these should allow a more accurate evaluation of the conservation status of the species, based recently on IUCN categories (IUCN 1994). The categories are based on: an observed population reduction (Criterion A); a reduced area of occupancy or extent of occurrence (Criterion B); population abundance (Criterion C); or probability

of extinction (Criterion D). There are no quantitative measures of population reduction, abundance or probability of extinction for *T. flaveola*, but the extent of occurrence is known (about 120 km²). The limit for Critically Endangered is an extent of occurrence less than 100 km², so that category is not appropriate, but Endangered (extent of occurrence less than 5000 km²) or Vulnerable (less than 20 000 km²) are both appropriate. For one of these conservation categories to be assigned based on Criterion B, information on at least two of the following are required:

- the number and fragmentation of locations;
- decline in abundance or extent of occurrence;
or
- fluctuations in abundance or extent of occurrence.

While there is no evidence of fluctuations in extent or abundance, it can be inferred that the known extent has declined. There is a record in the Wildlife Atlas at Mt Timbertop (8 km to the west of Mt Buller), collected in the late 1950s by Neboiss. Searching during 1994–95 around Mt Timbertop, and between Mt Timbertop and the closest currently known location, has consistently failed to confirm the presence of the species in this area. Either the original record is incorrect, or the species has disappeared from the general location (for some unknown reason).

Hence, the determination of conservation status is dependant on the number of subpopulations and the fragmentation of the population, which can be:

- Severely fragmented *or* known to exist at no more than 5 locations (Endangered); *or*
- Severely fragmented *or* known to exist at no more than 10 locations (Vulnerable). (*Note:* author's emphasis.)

The extent of fragmentation and the number of locations for aquatic stream-dwelling invertebrates is often difficult to determine. A 'location' is defined as 'a geographically or ecologically distinct area in which a single event (eg. pollution) will soon affect all individuals of the taxon present. A location usually, but not always, contains all or part of a subpopulation of the taxon, and is typically a small proportion of the taxon's total distribution' (IUCN 1994). 'Severely Fragmented' is defined as 'the situation where increased extinction risks to the taxon results from the fact that most individuals within a taxon are found in small and relatively isolated subpopulations. These small subpopulations may go extinct, with a reduced probability of recolonisation' (IUCN 1994).

The number of locations for the species based on the definition, is unclear. It could be argued that there are three distinct locations—the Delatite River, the King River and the Howqua River as geographically distinct areas—clearly making the species 'Endangered' under the IUCN classification. However, it is unlikely that a single event would affect all the individuals in one of these areas (with the exception perhaps of a widespread fire). A single event would be more likely to affect all individuals within a linear subcatchment, so it could also be argued from Fig. 1 that there are three locations within the King River catchment (numbered 1–3: see Table 1), three locations in the Howqua River catchment (4–6) and possibly eight locations within the Delatite River catchment (7–14)—giving a total of 14 locations.

This scenario places the species just outside the range for 'Vulnerable' (less than 10 locations) and suggests the appropriate IUCN classification would be 'Lower Risk Conservation Dependant' (defined as taxa which do 'not satisfy the criteria for any of the criteria Critically Endangered, Endangered and Vulnerable' but which are 'the focus for a continuing taxon specific or habitat specific conservation programme ..., the cessation of which would result in the taxon qualifying for one of the threatened categories above within a period of five years') or 'Lower Risk Near Threatened' (defined as taxa which do 'not qualify for Conservation Dependant, but which are close to qualifying for Vulnerable').

However, the criteria call for an evaluation of the number of locations or the degree of fragmentation. *Thaumatoperla flaveola* clearly has a fragmented distribution under the definition. Given that the species is restricted to the upper parts of each catchment, the chance of one of the locations becoming extinct is high. The Mt Buller–Stirling area is subject to a number of activities which could be detrimental to the species. Mt Buller is subject to significant alpine resort development

and activities. Less so Mt Stirling and the Razorback Spur area, but both timber harvesting and grazing are common there. Grazing can severely disturb the upper spring and seep areas of streams, resulting in the disappearance of at least one species (*Spathula tryssa*) from grazed spring heads (R. St. Clair, EPA, unpublished data). This would indicate that none of the populations are completely free from potential disturbance and extinction.

Given the low dispersal power of the adults, there would be little chance of recolonisation between sites in different subcatchments, should one of them go extinct. This would be especially true at those sites outside the Delatite River catchment (i.e. those in the King River and Howqua River catchments), where flying adults would be the only reasonable means of colonisation. Within the Delatite basin, there is a chance that recolonisation between subcatchments could occur through movement of the larvae along the stream lines, but even this would be relatively unlikely, given the distance between the sites.

Taken together, proximity of potentially threatening processes, the fragmented nature of the distribution, the observed reduction in extent of occurrence and the small total extent of occurrence (120 km²), the appropriate conservation status of the species under the guidelines of the IUCN would appear to be 'Endangered'.

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Number	Catchment	Creek name	Number	Catchment	Creek Name
1	King	Mine Ck	8	Delatite	Brown Ck
2	King	Fork Ck	9	Delatite	Falls Ck
3	King	unnamed	10	Delatite	Baldy Ck
4	Howqua	Stanley Ck	11	Delatite	Bluff Ck
5	Howqua	unnamed	12	Delatite	Delatite R.
6	Howqua	South Buller Ck	13	Delatite	Chalet Ck
7	Delatite	Currajong Ck	14	Delatite	Boggy Ck

Table 1. Creek names of the 14 possible 'locations' for *Thaumatoperla flaveola* as noted in Fig. 1.

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REFERENCES

- CNR, 1995. *Threatened Fauna in Victoria*. Department of Natural Resources & Environment, Melbourne.
- COMMONWEALTH OF AUSTRALIA, 1988. *Zoological Catalogue of Australia*. No. 6. *Ephemeroptera, Megaloptera, Odonata, Plecoptera, Trichoptera*. AGPS, Canberra.
- DOEG, T. J. & REED, J., 1995. Distribution of the Endangered Otway stonefly *Eusthenia nothofagi* (Plecoptera: Eustheniidae) in the Otway Ranges. *Proceedings of the Royal Society of Victoria* 107: 45-50.
- IUCN, 1994. *IUCN Red List Categories*. International Union for Conservation of Nature & Natural Resources, Gland, Switzerland.
- PETTIGROVE, V., 1991. *An investigation of the distribution and ecological requirements of the stonefly Thaumtoperla flaveola*. Report No. 104. Water, Materials & Environmental Science Branch, Rural Water Commission, Melbourne.
- TILLYARD, R. J., 1921. Revision of the family Eustheniidae (Order Perlaria) with descriptions of new genera and species. *Proceedings of the Linnaean Society of New South Wales* 46: 221-236.
- ZWICK, P., 1979. Revision of the stonefly family Eustheniidae (Plecoptera), with emphasis on the fauna of the Australian region. *Aquatic Insects* 1: 17-50.

BANKSIA INTEGRIFOLIA LINNEUS FIL. INFESTATION BY XYLORYCTID MOTH LARVAE, CAPE SCHANCK, VICTORIA

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ADAMS, R. & GEYER, H., 1999:07:31. *Banksia integrifolia* Linneus fil. infestation by xyloryctid moth larvae, Cape Schanck, Victoria. *Proceedings of the Royal Society of Victoria* 111(1): 93–102. ISSN 0035-9211.

Two species of xyloryctid moth have been identified, *Xylorycta paraboletta* Walker and *Scieropepla* sp., the larvae of which feed on the new leaf and branchlet tissue of *Banksia integrifolia* L. f. var. *integrifolia*. They appear to be specialist herbivores rather than seed predators, and the damage to *Banksia integrifolia* is predominantly canopy damage rather than a reduction in seed set. Infestations of these moth larvae on *Banksia integrifolia* are regionally patchy. The overall level of canopy damage in *Banksia integrifolia* woodland is relatively low (about 4%), but the level of inter-tree canopy damage is quite variable, and may be up to 10%. As the canopies appear to be able to recover from defoliation caused by xyloryctid moth larvae, interventionist management is not warranted. However, the low tree densities and increasing fragmentation of *Banksia integrifolia* woodland, coupled with repeated severe infestations of xyloryctid larvae, may still pose problems for the survival of existing mature trees in remnant *Banksia* woodland, and for the conservation of the two xyloryctid species.

BANKSIA integrifolia L. f. var. *integrifolia* woodland is still found growing over much of the Mornington Peninsula, but canopy dieback and periodic heavy infestations of moth larvae have raised concerns about the regeneration capacity and long term survival prospects of these remnant *Banksia* woodlands. However, little is known about the interactions between plant species and moths, and most Australian moths are wholly plant dependent (New 1992). It is still common for the presence of moths or their larvae to be treated simply as a damaging infestation by a pest species which needs to be controlled, and the impact of the infestation and the implications for moth species conservation is rarely considered. In evolutionary terms the Xyloryctinae is a relatively recent group which has radiated in Australia in association with *Acacia* and *Eucalyptus* (New 1984). As so little is known about plant–moth interactions, the conservation of these co-evolved species may need to receive more attention.

Xyloryctid moth larvae (Lepidoptera: Oecophoridae: Xyloryctinae) are specialist feeders on species from the families Myrtaceae and Proteaceae (Powell 1980), and cause substantial damage in *Banksia* species by tunnelling in the branchlets and inflorescences (Scott 1982; Zammit & Hood 1986; Wallace & O'Dowd 1989; Röhl & Woods 1994), and feeding on leaves (Common 1970; Common 1990). Reduced reproductive capacity caused by

insect larval damage to the inflorescence and seeds has been recorded in several species of *Banksia* (Scott 1982; Vaughton 1990), and associated with a number of lepidopteran and coleopteran species (Scott 1982; Hood 1985; Zammit & Hood 1986; Collins & Rebelo 1987; Wallace & O'Dowd 1989). Infestations of coleopteran larvae have also been recorded as a major contributor to the death of remnant *Banksia marginata* (Fearn 1989).

Two species of moth, *Xylorycta paraboletta* Walker and *Scieropepla* sp. (Lepidoptera: Oecophoridae: Xyloryctinae). (Nielsen et al. 1996), have been identified from the infested foliage of *Banksia integrifolia*. The larvae of both species feed on the new leaf and branchlet tissue of *Banksia integrifolia*. Both species of moth larvae were found to co-exist in the same shelter, and detailed examination of the larvae, cocoons and pupa, indicated that the two species were indistinguishable until the adult hatched.

Xyloryctid moth larvae weave web and ejected waste material into a nest-like shelter which is attached to the branchlets of *Banksia integrifolia*. The shelters vary in size; small shelters are about 8 cm wide and 5 cm deep, and large shelters may be up to 25 cm wide and 15 cm deep. As many as 66 larvae have been recorded from large shelters, and 20 from small shelters. Larvae were never observed outside the shelters. The final instar larva forms a cocoon-shaped structure of silk in

the shelter. This cocoon is a reddish-brown color, the same color as the shelter, but is more finely woven and has a soft down-like lining. It is fragile and easily torn open. The pupa are slender, delicate and light brown with a tapering posterior end.

Individual trees of all ages may become infested by larvae and covered in shelters, and canopy dieback may result (Fig. 1). Phytophagous insects are already well recognised as a significant contributor to canopy damage and to the general decline in health and population numbers of *Eucalyptus* species (Ohmart & Edwards 1991), but less is known about their role in the dieback of *Banksia* species.

Canopy dieback and infestation of *Banksia integrifolia* by moth larvae appears to be regionally patchy, and in 1986 and 1987 was restricted to the Main Creek area and some small areas at Point Leo, near Cape Schanek, Victoria (Fig. 2).

Populations of *Banksia integrifolia* at Mt Martha, on the northwestern side of the Peninsula, showed no visible signs of dieback or infestation. The infested area of Cape Schanek is open woodland, characterised by *Banksia integrifolia*, *Eucalyptus pauciflora* and *Leptospermum laevigatum*, on the relatively sheltered northeast slopes of coastal hills which descend to Main Creek. In mid 1986, it was estimated that about 65% of *Banksia integrifolia* individuals were infested, but that apparently uninfested trees were interspersed amongst infested trees. This patchiness is typical of the early stages of tree decline in *Eucalyptus* (Landsberg 1988) and may have been an early indicator of *Banksia* decline.

As it was likely that significant damage to the canopy and inflorescences of *Banksia integrifolia* was occurring on the Mornington Peninsula, and that some action to control the level of moth related



Fig. 1. Branchlets of *Banksia integrifolia* var. *integrifolia* heavily infested with xyloryctid larvae.

damage may be necessary, an assessment of the *Banksia integrifolia*-xylyoryctid moth association was carried out during 1986 and 1987. The study aimed to identify the species of moth(s) involved, and to determine the impact of moth infestation on the severity of canopy dieback, the regrowth of foliage, and the reproductive capacity of *Banksia integrifolia*.

METHODS

Moth identification and life cycle

Larval shelters from separate trees were collected from Main Creek (lat. $38^{\circ}29'$, long. $144^{\circ}56'$) at intervals between September 1986 and June 1987 and examined. Specimens required for measurements were removed from the shelter, killed in alcohol, and measured under $\times 40$ magnification using a graticule. Head capsule width and body length were measured for a total of 330 larvae.

A frequency distribution of head capsule width was used to indicate the number of larval instars, and the larval growth constant was determined using Dyar's law (Gillott 1980). A number of intact shelters were kept at a constant 10°C , and at room temperature (Scott 1982), to observe the development of larvae, pupa and adult moths. Moth species were identified by Dr E. Nielson, Division of Entomology, CSIRO, Canberra. Microscopic examination was also carried out to determine the presence of larvae in new normal foliage, new normal foliage regrowing from infested foliage, and dead inflorescences.

Dieback, infestation and regrowth of Banksia

Fourteen trees of *Banksia integrifolia* were tagged at Main Creek and at an uninfested population at Mt Martha (lat. $38^{\circ}17'$, long. $145^{\circ}00'$). Variables assessed at Main Creek were new normal leaf growth, new leaf growth after infestation, canopy

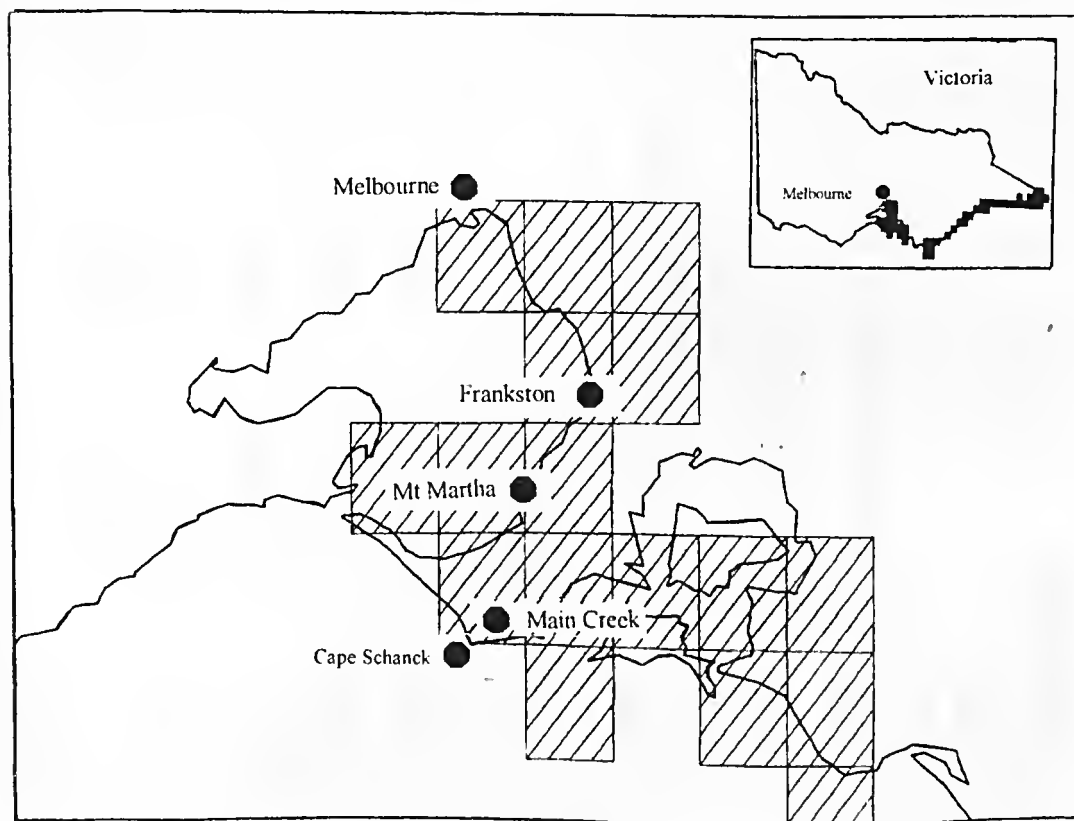


Fig. 2. Distribution of *Banksia integrifolia* var. *integrifolia* in Victoria (insert), and the location of the two study sites at Mt Martha (lat. $38^{\circ}17'$, long. $145^{\circ}00'$) and Main Creek (lat. $38^{\circ}29'$, long. $144^{\circ}56'$).

dieback, larval infestation, and shelter cover. All were scored as a percentage of the total canopy cover of each tree. Variables were recorded monthly between January and July 1987 at Main Creek. Tree girth was also recorded at Main Creek and used as an indirect measure of tree age. New normal leaf growth was estimated from the tagged trees at Mt Martha in January, February and July 1987. All percentages were arcsine transformed for analysis and display (Sokal & Rohlf 1995).

Reproductive capacity of Banksia

Twenty-four developing inflorescences on nine trees at Main Creek, and twelve inflorescences on four trees at Mt Martha were tagged, and their length measured from February 1987 to June 1987, when flowering finished. The number of developed follicles was counted on 11 of the tagged inflorescences at Main Creek and 12 tagged inflorescences at Mt Martha. A further 12 inflorescences were tagged at both sites in August 1986, the number of follicles counted and covered with a mesh bag to catch seeds which were released. Any of the tagged inflorescences which died or failed to complete flowering were examined microscopically for larval presence.

RESULTS

Moth identification and life cycle

Two species of moth, *Xylorycta parabollella* Walker and *Scieropepla* sp. (Lepidoptera : Oecophoridae : Xyloryctinae) (Nielsen et al. 1996), have been identified. However, determining the life cycle of the moths from specimens kept at 10°C constant temperature proved difficult as the larvae only survived within the shelter. Isolating larvae for observation resulted in reduced activity and appeared to slow down larval growth. Larvae which were observed for four months showed little change over this time. Observations of the pupa suggest that the moth emerged about one month after pupation, but there were too few observations to confirm this.

Six instars were indicated for both species. As the proportionate increase in head size from one instar to the next is constant (Dyar's law), instar head sizes should occur as discrete clusters of size rather than as a continuous range of head sizes. The frequency distribution of larval head capsule width indicates four definite clusters at 0.35, 0.5, 0.7, and 1.0 and two less pronounced clusters at 1.4 and 2.0 (Fig. 3).

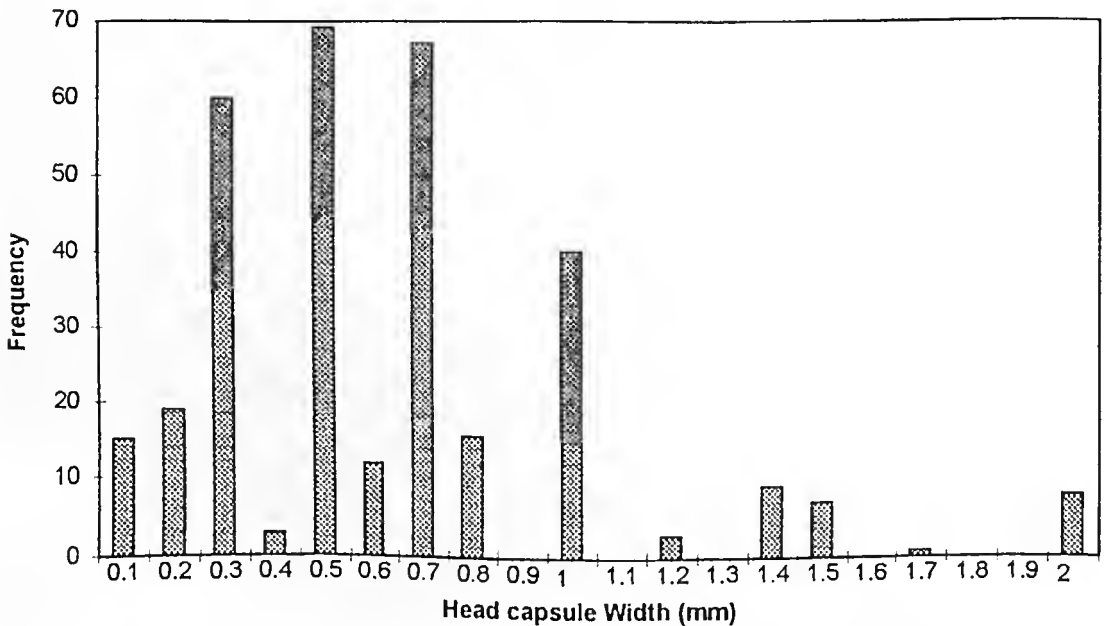


Fig. 3. Frequency distribution of the head capsule widths for larvae of *Xylorycta parabollella* and *Scieropepla* sp.

Although few pupa ($n=20$) were recovered from the shelters, two sizes were found; one 10 mm long and 2 mm diameter and one 7 mm long and 1.5 mm diameter. A small, fragile *Scieropepla* moth emerged from the small pupa and normal sized *Scieropepla* and *Xylorycta* from the larger pupa. It is not known if the small *Scieropepla* moth was the same species as the larger *Scieropepla* moth, but it is likely as sexual dimorphism is known for species in the Xyloryctinae (Nielsen & Common 1991).

The shelters contained many small larvae during January and February (Fig. 4) with predominantly 1st, 2nd and 3rd instars present. Relatively higher proportions of new foliage were produced during January and February (Fig. 5), and this appears to have provided suitable conditions for rapid

development of the larvae and a peak of pupation in March. Larvae in the 4th and 5th instar were generally present during March, April and May, and 6th instar larvae were present in June. A second pupation peak was also recorded for June (Fig. 6).

Dieback, infestation and regrowth of *Banksia*

The percentage of canopy dieback in *Banksia integrifolia* did not vary significantly from about 4% between February and July 1987 (mean = 4.0 ± 0.01), although dieback was significantly lower in January 1987 at about 1.7% (mean = 1.7 ± 0.07 , $df=89$, $p=0.006$). Canopy dieback was not correlated with tree age, as indicated by girth ($r=-0.32$; $p=0.271$, $df=12$), but was correlated with percentage infestation ($r=0.74$; $p=0.002$, $df=12$) and with percentage shelter cover ($r=0.63$; $p<0.001$, $df=54$).

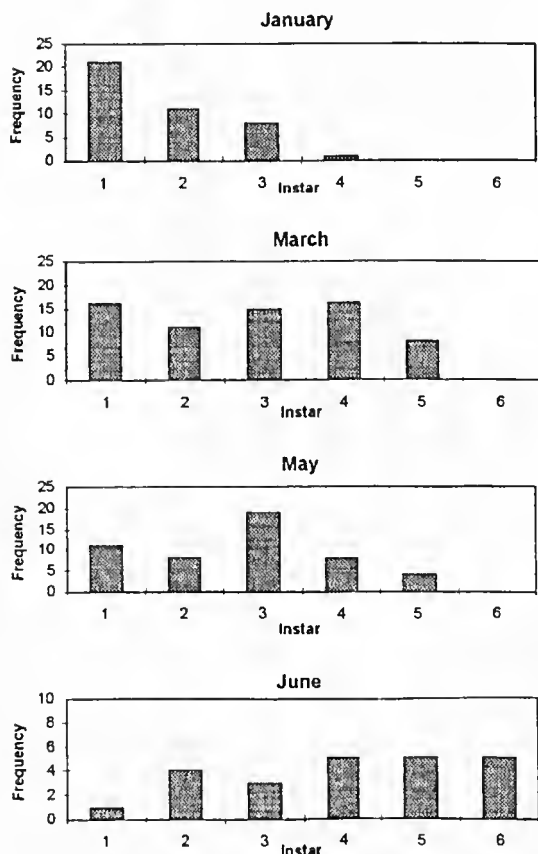


Fig. 4. Frequency of larval instars of *Xylorycta parabollela* and *Scieropepla* sp. for January, March, May and June 1987.

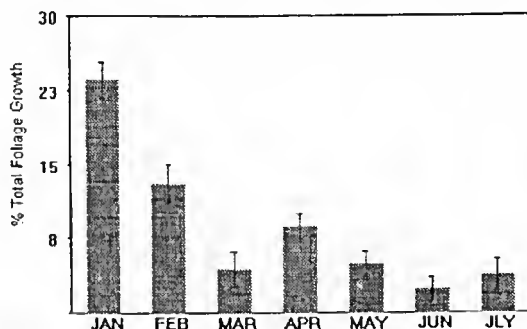


Fig. 5. Mean per cent (\pm s.e.) total foliage growth at Main Creek for January to July 1987. Percentages have been arcsine transformed.

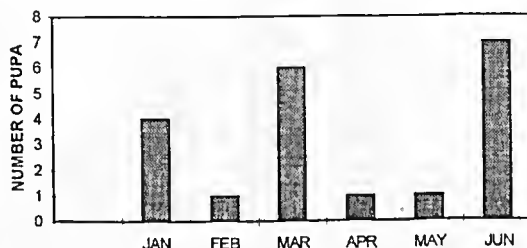


Fig. 6. Distribution by month of pupae ($n=20$) of *Xylorycta parabollela* and *Scieropepla* sp. recovered from shelters between January and June 1987.

New normal foliage growth of *Banksia integrifolia* at both Main Creek and Mt Martha began in November, and was measured between January and July 1987. Normal foliage growth virtually ceased during March to May, but trees at Main Creek had a second growth period in June–July (Fig. 7). This second growth period did not occur at Mt Martha. Generally, six buds appeared, of which five developed into leaves and the sixth into an inflorescence. The subsequent growth of branchlets was usually very rapid if unimpeded by infestation.

Larval infestation is associated with the availability of new leaf growth, and occurs after the numerous ovoid, opaque eggs are deposited in the leaf buds. The new leaf buds ceased to grow normally and became clumped and malformed (Fig. 1). The malformed tissue was very soft and spongy, and tunnelling was found in the stems and petioles of these malformed leaves. Tunnels were usually occupied by one larva, while many small larvae were found amongst the tightly clumped leaves. Numerous nematodes were also found in association with the malformed leaves. As the infestation developed, the larvae consumed the entire branchlet of new leaves. Regeneration arising from malformed, infested branchlets occurred in

February, March, April and May 1987 (Fig. 8), and these flushes of regeneration appeared to outgrow the infestation. Foliage suitable for larvae to feed on during the March–May period resulted almost entirely from regrowth of new foliage from infested branchlets, as the growth of new foliage from uninfested branchlets at Main Creek had decreased significantly from January through to May (Fig. 8).

Reproductive capacity of Banksia

The growth of the inflorescences at Main Creek and Mt Martha was rapid during February to April, but slowed during May and June as the inflorescences reached their final length and finished flowering. Flowering was complete by June at Main Creek, and by July at Mt Martha. There was no significant difference in the final size of inflorescences at either location (Table 1). Some of the tagged inflorescences at Main Creek died unexpectedly, and on examination, larvae were found tunnelling in the inflorescence rachis. Although *Scieropepla* larvae are known to tunnel in *Banksia* inflorescences (Common 1970; Scott 1982) these larvae did not appear to be xyloryetid larvae, and may have been a species of *Arotrophora*

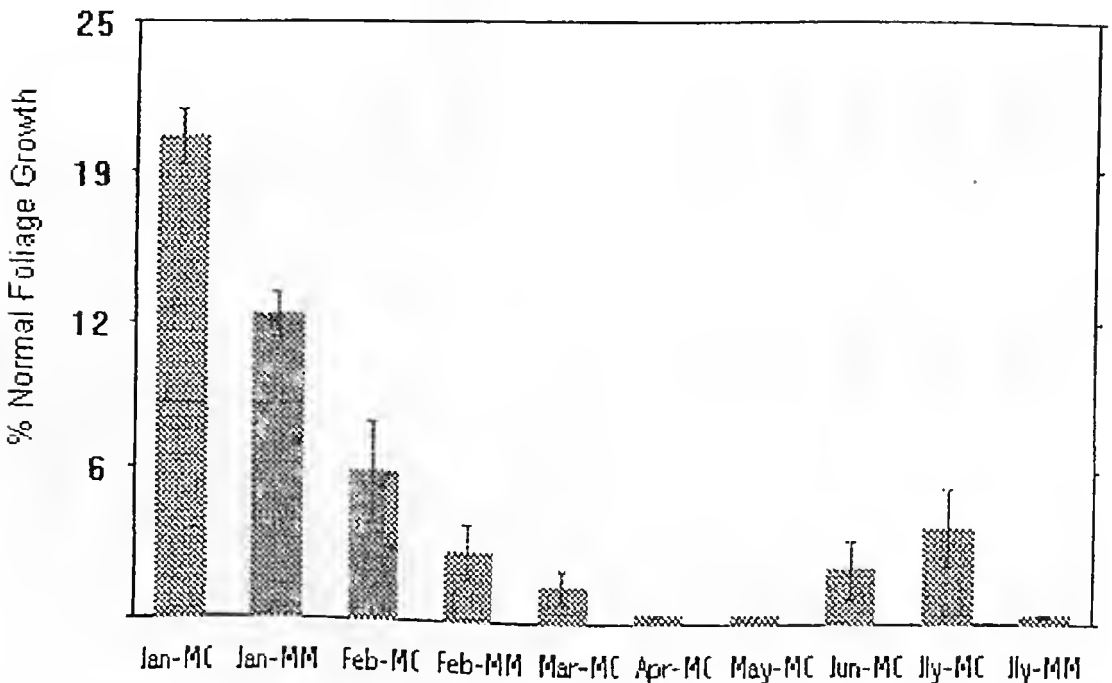


Fig. 7. Mean per cent (\pm s.e.) normal foliage growth for January to July 1987 for Main Creek (MC) and Mt Martha (MM). Percentages have been arcsine transformed.

larvae which are widespread and significant predators of *Banksia* inflorescences (Scott 1982; Zammit & Hood 1986; Wallace & O'Dowd 1989).

Quantifying seed production by catching released seeds in mesh bags was unsuccessful at Main Creek as the bags and some of the larger inflorescences were removed by vandals. Therefore a comparison of actual seed production between the infested and uninfested populations of *Banksia integrifolia* sites was not possible. However, seed capture at Mt Martha was successful with 10.2 ± 2.3 seeds per inflorescence recorded. It is also noteworthy that the developed foliicles of most of the tagged inflorescences ($n=24$) opened and released their seeds (Table 1). Reproductive capacity was estimated using the number of developed foliicles per inflorescence. The mean number of developed

foliicles per inflorescence produced by infested trees at Main Creek was not significantly different from the number produced by uninfested trees at Mt Martha (Table 1).

DISCUSSION

Two species of moth, *Xylorycta paraboletta* Walker and *Scieropepla* sp. (Lepidoptera: Xyloryctinae), have been identified from the infested foliage of *Banksia integrifolia*. Species from the Xyloryctinae have been positively associated with damaged inflorescences of *Banksia ericifolia* and *Banksia oblongifolia* (Zammit & Hood 1986), and *Banksia spinulosa* (Wallace & O'Dowd 1989), and several *Xylorycta* spp. have been recorded from *Banksia*

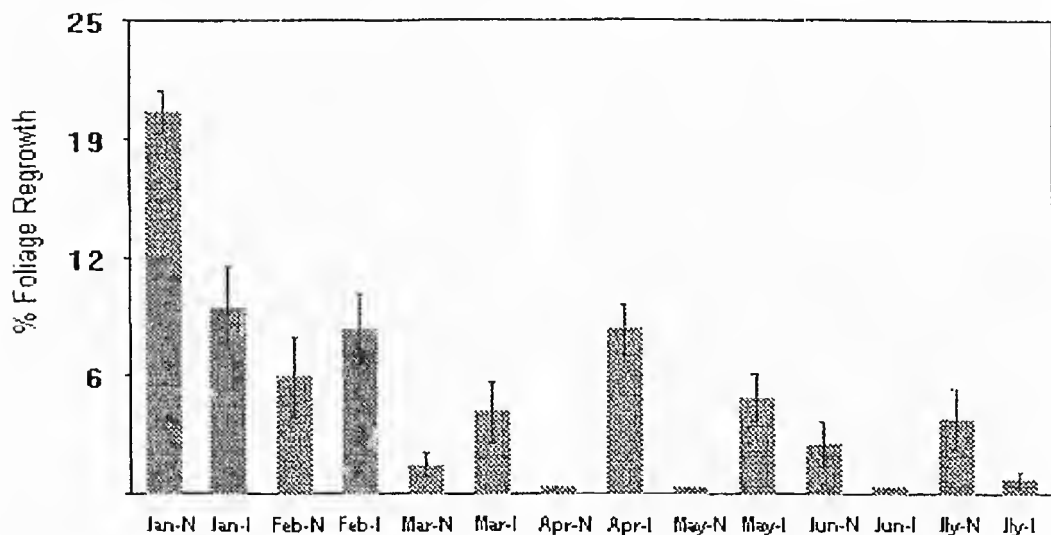


Fig. 8. Mean per cent (\pm s.e.) regrowth of infested (I) and non-infested (N) foliage at Main Creek for January to July 1987. Percentages have been arcsine transformed.

Inflorescence characteristics	Mt Martha	Main Creek	Significance ($p = 0.05$)
Open foliicles	27.4 ± 4.6 (12)	31.7 ± 6.4 (12)	ns
Closed foliicles	0.7 ± 0.4 (12)	3.9 ± 2.0 (12)	ns
Percentage open foliicles	98 ± 0.5 (12)	93 ± 1.0 (12)	ns
Seeds per inflorescence	10.2 ± 2.3 (12)	not available	—
Inflorescence length (mm)	75.4 ± 5.7 (11)	71.2 ± 3.8 (21)	ns
Developed foliicles per inflorescence	28.1 ± 4.5 (12)	35.6 ± 6.3 (11)	ns

Table 1. Mean (\pm s.e.) numbers of open and closed foliicles, the % open foliicles, and mean number of seeds per inflorescence for *Banksia integrifolia* var. *integrifolia*. Inflorescence length and number of developed foliicles (mean \pm s.e.) for uninfested (Mt Martha) and infested (Main Creek) trees of *Banksia integrifolia* var. *integrifolia*. Numbers of observations given in (); ns = $p > 0.05$.

littoralis, *B. grandis*, *B. telmatiaea* and *B. attenuata* (Scott 1982). However, they have usually been present in low numbers, and much of the seed and inflorescence damage seems to be caused by *Arotrophora* spp. (Lepidoptera: Tortricidae: Tortricinae) (Scott 1982; Zammitt & Hood 1986; Wallace & O'Dowd 1989; Röhl & Wood 1994) rather than *Xylorycta* spp. or *Scieropepla* spp. The main damage associated with a *Xylorycta* species was to the leaves and stems of *Banksia* rather than the flowers and seeds (*Xylorycta* sp. 5; Scott 1982). Results from Main Creek are consistent with this, as inflorescences which died unexpectedly were found to contain larvae which may have been a species of *Arotrophora* rather than xyloryetid species, but foliage and branchlet damage was always associated with *Xylorycta* sp. and *Scieropepla* sp.

Flowering and seed production in *Banksia* varies from year to year (McFarland 1985; Copland & Whelan 1989) and from species to species (Whelan & Burbidge 1980; Collins & Rubelo 1987; Copland & Whelan 1989). *Banksia integrifolia* is typical of the eastern Australian species, which flower in autumn (Collins & Rubello 1987). *Banksia integrifolia* L. f. var. *compar* (R. Br.) Bailey, flowers between February and June–July (McFarland 1985), and flowering for *Banksia integrifolia* L. f. var. *integrifolia* at Mt Martha and Main Creek was complete by June 1987. Short inflorescence lengths of 75.4 ± 5.7 mm and 71.2 ± 3.8 mm (Table 1) were also consistent with the 77.8 ± 3.6 mm recorded by McFarland (1985).

Seed production in *Banksia* is also highly variable (Scott 1982; Cowling et al. 1987). Seed set in Western Australian species can vary between 3 and 42 seeds per inflorescence (eg. table 1 in Cowling et al. 1987). Seed production per inflorescence for *Banksia integrifolia* L. f. var. *integrifolia* at Mt Martha (10.2 ± 2.3 ; Table 1) is low when compared to seed production for other eastern Australian species (22.9 ± 15.1 for *B. ericifolia* [Zammitt & Hood 1986]; 47.6 ± 4.0 for *B. spinulosa* [Vaughton 1990]). However, it is well within the overall seed production range for *Banksia*.

The degree of serotiny also varies. Strongly serotinous species (eg. *Banksia attenuata*, *B. serrata*, *B. spinulosa* var. *cunninghamii*) retain a significant proportion of the annual seed production in the canopy seed bank (Cowling et al. 1987; Lamont & Barker 1988) while weakly or non-serotinous species (eg. *Banksia integrifolia*, *B. marginata* and *B. menziesii*) release seed as it ripens (Wrigley & Fagg 1989). Viable *Banksia* seed does not accumulate in the soil (Cowling et al. 1987; Specht 1994) and successful regeneration of *Banksia* relies

on canopy stored seed in serotinous species, or on adequate annual seed production in weakly serotinous species. Between 93% and 98% of developed folioles of *Banksia integrifolia* at both Main Creek and Mt Martha opened and released seed, confirming the low levels of canopy stored seed and the dependence of *Banksia* woodland regeneration on annual seed production. Weakly serotinous species also tend to have higher levels of seed predation (Cowling et al. 1987), and any loss of *Banksia integrifolia* seed due to xyloryetid moth damage has the potential to reduce the long term regeneration capacity of the species.

Although no counts of seeds per inflorescence were available for Main Creek, the impact of xyloryetid moth infestation on reproductive capacity can be estimated using the number of developed folioles as a measure of seed set (Whelan & Burbidge 1980; Paton & Turner 1985; Copland & Whelan 1989; Wallace & O'Dowd 1989). Reproductive capacity does not appear to be reduced in infested trees, as the number of developed folioles per inflorescence (Table 1) and the number of open folioles per inflorescence at Main Creek was not significantly different from the number at Mt Martha (Table 1). As Cowling et al. (1987) suggest that insect-damaged folioles in weakly serotinous species do not open, it could be argued that opened folioles on inflorescences at Main Creek had successfully produced and released seed, and that the numbers of seeds per inflorescence at Main Creek was comparable with Mt Martha. That is, the infestation of xyloryetid moths at Main Creek had not reduced seed production beyond the background level of seed predation losses.

Overall canopy damage for the *Banksia integrifolia* woodland at Cape Sehanek was quite low, at about 4%. However, there was considerable variation between trees, ranging from no dieback in uninfested trees through to between 1% and 10% dieback in infested trees. Canopy dieback was not related to tree age and it is unlikely to be a response to plant stress or low resource availability (Landsberg & Gillison 1995). Up to 36% canopy damage caused by salt spray has been recorded for *Banksia integrifolia* in coastal situations (Morris 1992), however, as the infested area of *Banksia integrifolia* at Cape Sehanek occupies northeast slopes which are relatively sheltered from the prevailing southerly and westerly winds, the observed canopy dieback is unlikely to result from salt spray.

Canopy damage caused by insect herbivores is well recognised for many *Eucalyptus* species (Ohmart & Edwards 1991), and the microlepidopteran group Oecophoridae, to which *Xylorycta*

and *Sceiropepla* belong, is one of the most common groups of eucalypt defoliators (Ohmart et al. 1983) and leaf-litter decomposers (Common 1980). *Xyloryctia* and *Sceiropepla* are considered to be specialist herbivores on *Banksia* (Powell 1980; Nielsen & Common 1990), and the high positive correlations between canopy dieback and the proportions of tree infestation and shelter cover strongly support the proposal that it is infestation by these species which is responsible for the canopy damage in *Banksia integrifolia*.

The larvae of both *Xyloryctia parablella* and *Sceiropepla* sp. feed on the new leaf and branchlet tissue of *Banksia integrifolia*, and eventually consume the entire branchlet. Foliage suitable for xyloryctid larvae to feed on resulted almost entirely from flushes of new growth. Similar relationships have been reported (eg. Carne 1965, in Landsberg 1988), and infested or dieback trees also tend to produce more new foliage, and out-of-season regrowth, as a response to prior infestation (Landsberg 1988). It is possible that this regrowth foliage represents a different quality food source for the larvae (Landsberg 1990), and it may be preferred as oviposition sites (Wileox & Crawley 1988). However, the malformation of leaves of *Banksia integrifolia* may be caused by nematodes rather than the xyloryctid larvae. Nematodes were found in association with moth eggs and larvae, and a similar association between the gall-forming nematode *Fergusobia currie* and the fly *Fergusonia nicholsoni* has been recorded in *Eucalyptus* (Currie 1937).

Normal foliage growth was negligible during autumn and early winter, but the regeneration of foliage on infested trees was prolific. The subsequent growth of branchlets was usually very rapid, and frequently outgrew the infestation. This suggests that *Banksia integrifolia* is able to recover, at least in the short term, from the defoliation caused by xyloryctid moth larvae, and that active management to reduce the levels of larval infestation is not warranted. However, given the likelihood of re-infestation of regrowth foliage (Landsberg 1990), the longer term impacts of repeated re-infestation on tree canopy dieback and overall tree health need to be assessed. Although xyloryctid moth infestation does not appear to reduce seed set, and individual trees are able to recover from canopy damage, repeated infestation may still pose a threat to the survival of these *Banksia integrifolia* remnants, and to the xyloryctids themselves through loss of their host species. The extent and seasonality of infestation by xyloryctids over the whole of the range of *Banksia integrifolia* var. *integrifolia*, and the

degree of dependence of these moth species on *Banksia*, also need to be determined. Moth infestation should not be viewed as a simple pest problem requiring control, and future management of *Banksia* woodland needs to emphasise habitat integrity for *Banksia*, so both *Banksia* and these xyloryctid moths species survive in the long term.

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REFERENCES

- COLLINS, B. G. & REBELO, T., 1987. Pollination biology of the Proteaceae in Australia and southern Africa. *Australian Journal of Ecology* 12: 387-421.
- COMMON, I. F. B., 1970. Lepidoptera. In *The Insects of Australia*, CSIRO, Melbourne University Press, Melbourne, 822-824.
- COMMON, I. F. B., 1980. Some factors responsible for imbalances in the Australian fauna of Lepidoptera. *Journal of the Lepidopteran Society* 34: 286-294.
- COMMON, I. F. G., 1990. *Moths of Australia*, Melbourne University Press, vi + 535 pp., 32 pls.
- COPLAND, B. J. & WHELAN, R. J., 1989. Seasonal variation in flowering intensity and pollination limitation of fruit set in four co-occurring *Banksia* species. *Journal of Ecology* 77: 509-523.
- COWLING, R. M., LAMONT, B. B. & PIERCE, S. M., 1987. Seed bank dynamics of four co-occurring *Banksia* species. *Journal of Ecology* 75: 289-302.
- CURRIE, G. A., 1937. Galls of *Eucalyptus* trees. A new type of association between flies and nematodes. *Proceedings of the Linnean Society of New South Wales* 62: 147-174.
- FEARN, S., 1989. Some observations on the habits of *Paroplitus australis* (Erichson) (Coleoptera: Cerambycidae, Prioninae) and its damaging effects on the food plant *Banksia marginata* Cav. in Tasmania. *Australian Entomological Magazine* 16: 81-84.
- GILLOTT, C., 1980. *Entomology*, Plenum Press, New York, xviii + 729 pp.
- HOOD, C., 1985. The arthropod community associated with *Banksia* inflorescences. *Circular of the Entomological Society of New South Wales* 355: 36-40.
- LAMONT, B. B. & BARKER, M. J., 1988. Seed bank dynamics of a serotinous, fire-sensitive *Banksia* species. *Australian Journal of Botany* 36: 193-203.

- LANDSBERG, J., 1988. Dieback of rural eucalypts: tree phenology and damage caused by leaf-feeding insects. *Australian Journal of Ecology* 13: 251–267.
- LANDSBERG, J., 1990. Dieback of rural eucalypts: does insect herbivory relate to dietary quality of tree foliage? *Australian Journal of Ecology* 15: 73–87.
- LANDSBERG, J. & GILLIESON, D. S., 1995. Regional and local variation in insect herbivory, vegetation and soils of eucalypt associations in contrasted landscape positions along a climatic gradient. *Australian Journal of Ecology* 20: 299–315.
- McFARLAND, D. C., 1985. Flowering biology and phenology of *Banksia integrifolia* and *B. spinulosa* (Proteaceae) in New England National Park, NSW. *Australian Journal of Botany* 33: 705–714.
- MORRIS, E. C., 1992. Canopy damage to native vegetation on the central coast of New South Wales: current status and detection of future changes. *Australian Journal of Ecology* 17: 141–154.
- NEW, T. R., 1984. *Insect Conservation: An Australian Perspective*, W. Junk, Dordrecht, xiii + 184 pp.
- NEW, T. R., 1992. *Introductory Entomology for Australian Students*, New South Wales University Press, Kensington, ix + 258 pp.
- NIELSEN, E. S. & COMMON, I. F. B., 1991. Lepidoptera. In *The Insects of Australia*, 2nd edn, CSIRO, Melbourne University Press, 817–915.
- NIELSEN, E. S., EDWARDS, E. D. & RANGSI, T. V., 1996. *Checklist of the Lepidoptera of Australia*, CSIRO, Australia, xiv + 529 pp, 1 CD-ROM.
- OHMART, C. P. & EDWARDS, P. B., 1991. Insect herbivory on *Eucalyptus*. *Annual Review of Entomology* 36: 637–657.
- OHMART, C. P., STEWART, L. G. & THOMAS, J. R., 1983. Phytophagous insect communities in the canopies of three *Eucalyptus* forest types in southeastern Australia. *Australian Journal of Ecology* 8: 395–403.
- PATON, D. C. & TURNER, V., 1985. Pollination of *Banksia ericifolia* Smith: birds, mammals and insects as pollen vectors. *Australian Journal of Botany* 33: 271–286.
- POWELL, J. A., 1980. Evolution of larval food preferences in microlepidoptera. *Annual Review of Entomology* 25: 133–159.
- RÖHL, L. J. & WOODS, W., 1994. Biological and insecticidal control of *Arotrophora arcuatalis* (Walker) (Lepidoptera: Tortricidae): an important pest of banksias in Western Australia. *Plant Protection Quarterly* 9: 20–23.
- SCOTT, J. K., 1982. The impact of destructive insects on reproduction in six species of *Banksia* L. f. (Proteaceae). *Australian Journal of Zoology* 30: 901–921.
- SOKAL, R. R. & ROHLF, F. J., 1995. *Biometry. The Principle and Practice of Statistics in Biological Research*, W. H. Freeman & Co., New York, xix + 887 pp.
- SPEIGHT, R. L., 1994. Heathlands. In *Australian Vegetation*, R. H. Groves, ed., Cambridge University Press, Melbourne, 253–275.
- VAUGHTON, G., 1990. Predation by insects limits seed production in *Banksia spinulosa* var. *neoanglica* (Proteaceae). *Australian Journal of Botany* 38: 335–340.
- WALLACE, D. D. & O'DOWD, D. J., 1989. The effects of nutrients and inflorescence damage by insects on fruit-set by *Banksia spinulosa*. *Oecologia* 79: 482–488.
- WHEELAN, R. J. & BURBIDGE, A. H., 1980. Flowering phenology, seed set and bird pollination of five Western Australian *Banksia* species. *Australian Journal of Ecology* 5: 1–7.
- WILCOX, A. & CRAWLEY, M. J., 1988. The effects of host plant defoliation and fertilizer application on larval growth and oviposition behaviour in cinnabar moth. *Oecologia* 76: 283–287.
- WRIGLEY, J. W. & FAGG, M., 1989. *Banksias, Waratahs and Grevilleas*, Collins Publishers, Sydney, 584 pp.
- ZAMMIT, C. & HOOD, C. W., 1986. Impact of flower and seed predators on seed-set in two species of *Banksia* shrubs. *Australian Journal of Ecology* 11: 187–193.

THE TURRIFF METEORITE FROM VICTORIA, AUSTRALIA

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The Turriff meteorite is a new L5 chondrite found near the township of Turriff, in north-western Victoria, Australia, in 1994. The single 218 g stone has a near-complete fusion crust altered to goethite. The meteorite contains abundant well-defined chondrules, together with blebs of troilite, kamacite and rare taenite, set in a recrystallised matrix consisting mainly of low-Ca orthopyroxene, olivine and plagioclase. Microprobe analyses of the olivine (Fo₇₆) and orthopyroxene (Fo₂₆) are typical of L5 chondrites. The meteorite shows no evidence of shock features (S1 on scale) and is relatively low on the scale of weathering (W0–W1), with veinlets of iron oxide permeating the matrix. The Turriff meteorite is the eleventh meteorite recorded in Victoria.

Key words: Turriff meteorite, Victoria, L5 chondrite.

THE TURRIFF meteorite is a new L5 chondrite, discovered in a ploughed paddock in northwestern Victoria's Mallee region in 1994. The find site (35°29.7'S, 142°37.3'E) is about 13 km ESE of the township of Turriff, in flat, semi-arid, wheat-farming country with a sandy soil covering (Fig. 1). The find was made by Mr David Rowney, who sold the meteorite to Museum Victoria early in 1997. Its registered number is E14405. The name and the data required for classification have been approved by the Nomenclature Committee of the Meteoritical Society (in Grossman 1998). The Turriff meteorite is only the eleventh recorded meteorite from Victoria.

DESCRIPTION

The meteorite is a 6-sided, slightly tapering, reet-angular block with rounded edges, dimensions of 7 × 4.5 × 3.5 cm and a mass of 218 g (Fig. 2). The original fusion crust has completely altered to goethite showing a dimpled surface and well-preserved shrinkage fractures. The crust was complete except for two small regions at the narrow end of the stone. A slice taken from this end was used to make a polished thin section.

The internal portion of the meteorite shows abundant dark grey chondrules set in a white, partly friable matrix. In thin section, the chondrules are distinct and consist mainly of granular olivine/

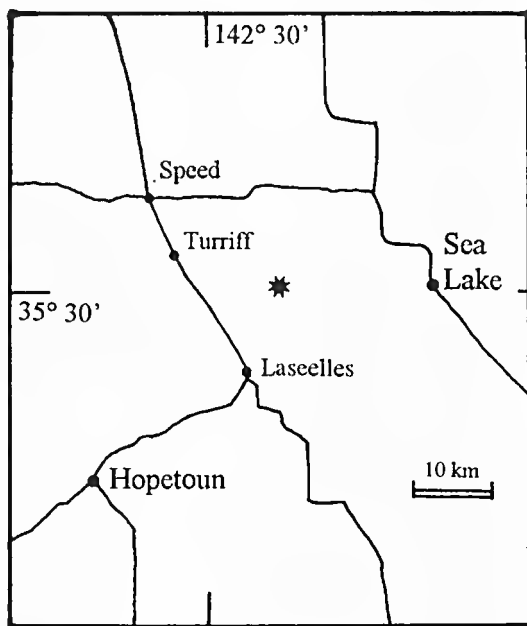


Fig. 1. Location map showing find site for the Turriff meteorite (*).



orthopyroxene/plagioclase and barred orthopyroxene/plagioclase intergrowths. They range in diameter mainly between 0.3 and 1.5 mm, with a few larger ones reaching 2.5 mm across. The recrystallised matrix contains angular to slightly rounded grains of orthopyroxene and olivine, with minor amounts of plagioclase and grains and blebs of troilite, kamacite and taenite. The olivine grains show sharp extinction and irregular fractures. Of the opaque minerals, troilite is the most common, forming ragged grains and patches up to 0.5 mm across. Kamacite grains are more common and larger (up to 0.5 mm across) than taenite. Veinlets of iron hydroxide permeate the matrix. Clinopyroxene and chromite were not detected.

Microprobe analyses were obtained on the main phases using a Cameca SX50 instrument operating at 15 kV and a 25 μ m beam current, and using natural and synthetic standards (see Table 1). The olivine in both the chondrules and the groundmass is homogeneous in composition, with an average formula of $\text{Fo}_{75.8}\text{Fa}_{23.7}\text{Te}_{0.5}$, i.e. $100(\text{Fe}+\text{Mn})/(\text{Fe}+\text{Mn}+\text{Mg}) = 24$ (% mean deviation in Fe = 2). The low-Ca orthopyroxene is Mg-rich with an average composition expressed as $\text{En}_{78.3}\text{Fs}_{20.2}\text{Wo}_{1.5}$ (% mean deviation in Fe = 2.5 %). The plagioclase composition is in the range oligoclase-andesine. The kamacite is quite uniform in composition, with Fe/Ni ranging between 13.5 and 15.1. Taenite is rich in nickel, with Fe/Ni varying between 0.98 and 1.96.

CLASSIFICATION

A full chemical analysis of the Turriff meteorite was not carried out, but the meteorite may be classified on textural and mineralogical grounds. Based on the above features, and according to the chondrite classification criteria of Dodd (1981) and Van Schmus & Wood (1967), the Turriff meteorite is a borderline L5–6 chondrite. However, the Wo content of the orthopyroxene is typical of the range shown by L5 chondrites (Scott et al. 1986). The absence of undulose extinction and planar fractures in olivine indicates the meteorite is unshocked (S1 on the scale of Stöffler et al. 1991). The meteorite shows features characteristic of W0–W1 weathering (on the scale of Wlotzka 1993), suggesting a relatively young fall, perhaps of the order of a few thousand years or less.

	1	2
SiO_2	38.53	55.50
TiO_2	—	0.14
Al_2O_3	—	0.14
Fe_2O_3	—	—
Cr_2O_3	0.04	0.14
NiO	0.03	0.04
FeO	21.57	13.34
MnO	0.50	0.53
MgO	38.41	28.52
CaO	—	0.70
Na_2O	—	—
K_2O	—	—
Total	99.08	99.05

Table 1. Microprobe analyses of silicate minerals in the Turriff meteorite. 1 = average olivine in chondrules and matrix (5 grains); 2 = average opx in chondrules and matrix (10 grains).

CONCLUSION

There are few similar L5–6 meteorites recorded from the Mallee region of Victoria, although the semi-arid, flat terrain and sandy soils lend themselves to meteorite preservation. The Bealiba meteorite (Birch 1991) was found some 180 km to the southeast of Turriff, and the Kulnine meteorite (Walcott 1915) some 150 km to the NNW. Bealiba and Turriff are superficially similar meteorites, but show slight differences in mineralogy (for example, in Bealiba olivine is $\text{Fo}_{74.4}$ and orthopyroxene is $\text{Fs}_{22.5}$), while Kulnine shows unusual chemical and textural features (Mason 1973).

ACKNOWLEDGEMENTS

I am grateful to Dermot Henry for his help with the investigation of the meteorite. Microprobe analyses were obtained in the School of Earth Sciences, University of Melbourne, with the assistance of David Steele. Alex Bevan, Curator of Meteorites at the Western Australian Museum, kindly read an early version of the manuscript.

Fig. 2. Photograph of Turriff meteorite (7 cm high).

REFERENCES

- BIRCH, W. D., 1991. The Bealiba Meteorite from Victoria. *Proceedings of the Royal Society of Victoria* 103(1): 7-11.
- DODD, R. T., 1981. *Meteorites. A Petrologic-Chemical Synthesis*. Cambridge University Press, 368 pp.
- GROSSMAN, J., ed., 1998. Meteoritical Bulletin, No. 82. In *Meteoritics*, 33.
- MASON, B., 1973. Notes on Australian meteorites. *Records of the Australian Museum* 29: 169-181.
- SCOTT, E. R. D., TAYLOR, G. J. & KEIL, K., 1986. Accretion, metamorphism and brecciation of ordinary chondrites: evidence from petrologic studies of meteorites from Roosevelt County, New Mexico. *Proceedings of the Seventeenth Lunar and Planetary Science Conference, Pt 1. Journal of Geophysical Research* 91: B13, E115-123.
- STÖFFLER, D., KEIL, K. & SCOTT, E. R. D., 1991. Shock metamorphism of ordinary chondrites. *Geochimica et Cosmochimica Acta* 55: 3845-3867.
- VAN SCHMUS, W. R. & WOOD, J. A., 1967. A chemical-petrologic classification for the chondritic meteorites. *Geochimica et Cosmochimica Acta* 31: 745-765.
- WALCOTT, R. H., 1915. Descriptions of the Victorian meteorites, with notes on obsidianites. *Memoirs of the National Museum of Victoria* 6: 3-66.
- WLOTZKA, F., 1993. A weathering scale for the ordinary chondrites (Abstract). *Meteoritics* 28: 460.

ROANELLA, A NEW ?BILLINGSSELLOID BRACHIOPOD
FROM THE LATE CAMBRIAN DOLODROOK LIMESTONES,
EAST-CENTRAL VICTORIA

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Brock, G. A. & Talent, J. A., 1999:07:31. *Roanella*, a new ?billingselloid brachiopod from the Late Cambrian Dolodrook limestones, east-central Victoria. *Proceedings of the Royal Society of Victoria* 111(1): 107–120. ISSN 0035-9211.

The new brachiopod genus *Roanella* is described from a large collection of silicified shells collected from Upper Cambrian (Idamean) limestones in the vicinity of Roan Horse Gully in the Dolodrook River watershed. The taxon is very similar to *Billingsella*, but is distinguished from it by the presence of a deltidium (rather than a pseudodeltidium) and absence of dental plates. The presence of a deltidium in *Roanella* is unique for the Billingselloidea. The restricted facies distribution, high density clustering, limited lateral and stratigraphic extent and high disarticulation index indicate *R. platystrophioides* was an opportunistic species that inhabited a high energy, shallow marine environment.

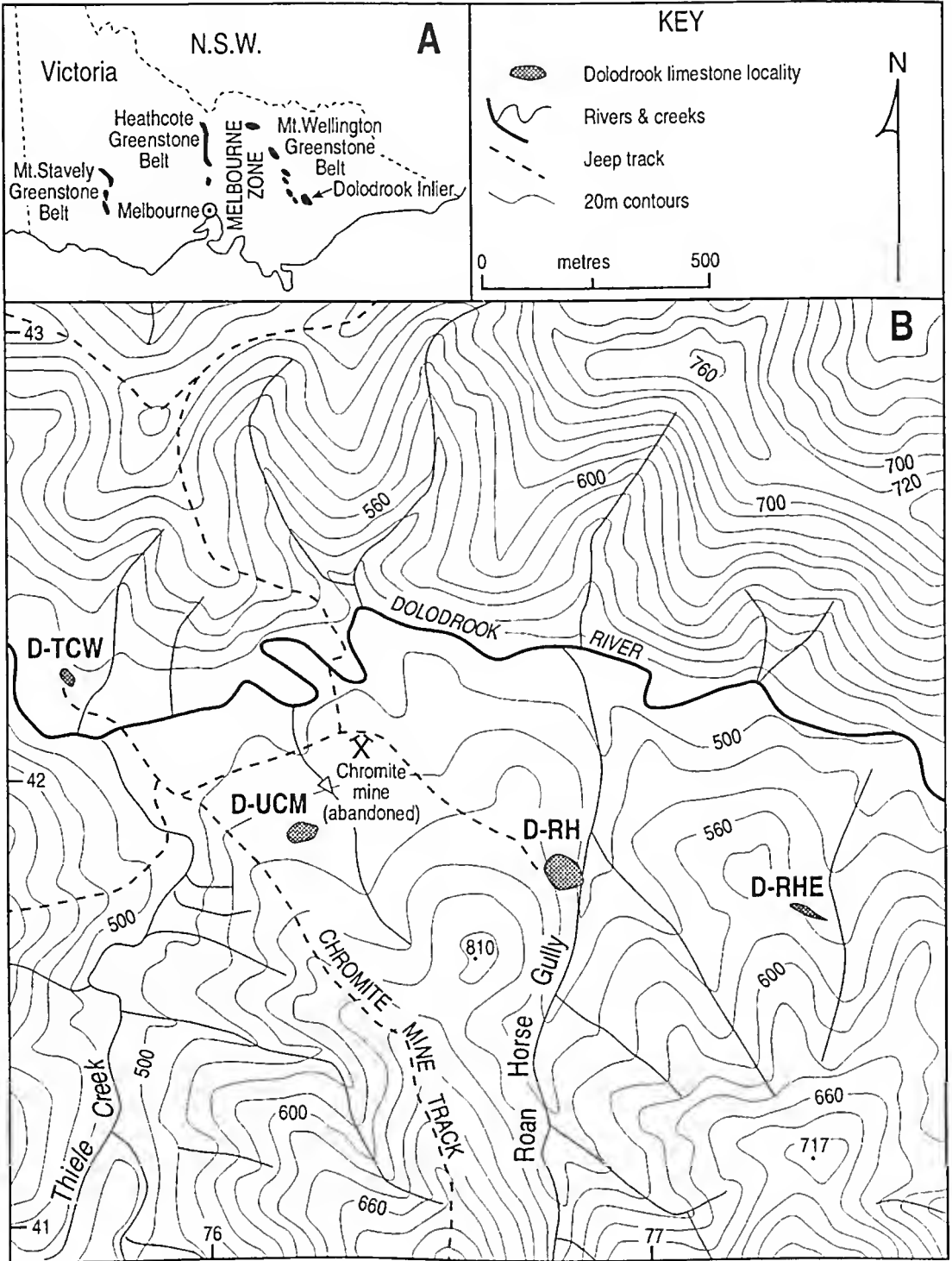
Key words: Upper Cambrian, Dolodrook limestone, Brachiopoda, *Roanella*, taxonomy.

CAMBRIAN fossiliferous localities in Victoria are almost exclusively restricted to small fault-bounded units, often with limited exposure, associated with the Heatheote and Mt Wellington greenstone belts, defining the western and eastern margins respectively of the Melbourne Zone (Crawford & Keays 1978; Crawford 1988) in the southwestern Laichlan Fold Belt (Glen 1992: fig. 2). The earliest descriptions of Cambrian fossils from Victoria focussed on the faunas of the *Dinesus* and *Amphoton* beds in the 150 m thick Knowsley East Formation in the Heatheote Greenstone Belt. These produced trilobites (Etheridge 1896; Gregory 1903; Chapman 1917; Öpik 1949), brachiopods and bivalves (Chapman 1904, 1917), and a relatively diverse dendroid graptolite assemblage (Chapman & Thomas 1936). Limestone bodies, some perhaps fault-bounded, of Middle–Late Cambrian age in the Dolodrook River Inlier of the Mt Wellington Greenstone Belt contain a diverse shelly fauna including trilobites (Harris & Thomas 1954; Thomas & Singleton 1956), lingulate brachiopods (Engelbreiten, in prep.), calcate brachiopods, molluses, crinoids and algae (partly described by Chapman 1907, 1911). These faunas are either in need of revision or have not been formally described. As an initial step in this direction, the articulate brachiopod *Roanella platystrophioides* (Chapman) is redescribed, based on a large collection of silicified shells from three localities in the vicinity of Roan Horse Gully, a tributary of the Dolodrook River (Fig. 1).

PREVIOUS INVESTIGATIONS

Initial investigations into the geology and physiography of the Dolodrook River–Mt Wellington–Macallister River area were undertaken by R. A. F. Murray (1879) and A. W. Howitt (1891), but it was E. O. Thiele (later Teale) who, during a series of reconnaissance excursions to the region (Thiele 1905–1908), first called attention to the Dolodrook limestones (Thiele 1907: 26) initially mapping them as Silurian units resting on top of, and surrounded by, Ordovician graptolite shales. The Silurian age was supported at the time by Chapman's (1907) identification of *Platystrophia bifurcata* (= *Roanella platystrophioides* herein). Teale (1920) later provided a comprehensive synthesis of the stratigraphy, geology and palaeontology of the region, revising much of his earlier work. The discovery of early Palaeozoic trilobites in four of nine limestone occurrences in the Dolodrook River watershed (Thiele 1908; Teale 1920; Chapman 1911), led Thiele to assume a broad Cambrian age for all the limestone occurrences in that area.

Teale (1920) recognised three groups of rocks in his pre-Ordovician (or Heatheotian) Series: pre-Upper Cambrian Serpentine, overlain unconformably by the Upper Cambrian trilobite (or Dolodrook) limestones, and bedded ash and tuffs, his Garvey Gully series, which he considered to be interbedded with the limestones (Teale 1920: 78).



Harris & Thomas (1954: 36) revised some of Teale's (1920) conclusions, indicating that the serpentine was probably 'not an older series but an essential part of the Cambrian sequence'. Apart from recovering Middle Ordovician graptolites from near the mouth of Roan Horse Gully and adding substantially to knowledge of graptolites in the area, Harris & Thomas (1954) also provided a list of trilobites identified by O. P. Singleton from the limestones at Roan Horse Gully and a locality on the Dolodrook River upstream from Black Soil Gully (see also Thomas & Singleton 1956). Little subsequent work has been undertaken in the region, apart from an unpublished honours thesis (Duddy 1974), though reference has been made to the area in broad regional syntheses (eg. VandenBerg 1988; Crawford 1988).

GEOLOGICAL SETTING

The geology of the Dolodrook Inlier, presented in meticulous detail by Teale (1920) has been modified in relatively minor ways by Harris & Thomas (1954), Duddy (1974) and Crawford & Keays (1978). It is part of the Mt Wellington Greenstone Belt (Fig. 1A), and outcrops as a broad, NW-SE striking, anticlinorial structure with a core of serpentinised cumulate ultramafic rocks, including harzburgites and dunites (Crawford et al. 1984; Nelson et al. 1984; Crawford 1988); partially serpentinised conglomerates are also known (Crawford 1988). Cas (1983) argued that the Victorian greenstone belts were produced in intracratonic rift zones, but Crawford et al. (1984), Crawford & Keays (1987) and Crawford & Berry (1992: 38) have argued, based on comparison with modern western Pacific analogues, that the greenstones formed in an intra-oceanic arc and backarc setting, and were subsequently thrust craton-wards at some time prior to the Middle Devonian. Collins & Vernon (1994: 260, fig. 3a, b) have recently provided two models to explain development of the southern Lachlan Fold Belt: a sequential back-arc formation model, and a back-arc duplicate model involving strike-slip faulting.

The ultramafics are unconformably overlain by

the Garvey Gully Formation, an approximately 200 m thick unit of fine to medium-grained, poorly sorted green to grey volcanolithic sandstones, minor conglomerates and shales. Rounded monomineralic and polymineralic clasts are relatively common towards the base of the unit and are assumed to have been derived, in the main, from the underlying greenstone terrane (Duddy 1974; Crawford 1988: 54). The sandstones produce rare fragmentary echinoderm plates and crinoid ossicles and display various soft sediment structures including small scale crossbedding, scour surfaces, slumps, flame structures and channels (Duddy 1974) indicating deposition in a 'high energy', shallow marine setting.

The Dolodrook River limestones have been regarded as a thin, autochthonous unit interbedded within the upper part of the Garvey Gully Formation (Teale 1920; Duddy 1974; VandenBerg 1988; Crawford 1988). No type section appears to have been nominated. Lithological boundaries between the limestone outcrops and the Garvey Gully Formation are almost always obscured by soil cover or by localised faulting, but Duddy (1974) has reported the presence of a disconformable contact between the Garvey Gully Formation and overlying Dolodrook River limestone at his locality 109, in Black Soil Gully West. He (Duddy 1974) and subsequent authors, assumed no major stratigraphic break between the units. In accord with this view, VandenBerg (1988: 17, table 3-1) indicated the Dolodrook River limestone as a lithostratigraphic member of the Garvey Gully Formation, except that the latter is inferred by us (see below) to be mid-Ordovician rather than Cambrian in age. Recent discoveries of *Diplograptus* and *Didymograptus* from a locality in the Garvey Gully Formation arenites within metres, and along strike, from the Dolodrook River limestone (D-TCW) at Thiele's Creek (Fig. 1B), indicate a mid-Ordovician (Darriwilian) age for the formation. This previously unrecorded age discrepancy between the Cambrian limestones and the Ordovician Garvey Gully Formation can be adequately accounted for if the limestones are viewed as submarine carbonate channel deposits and/or debris flows and isolated olistoliths derived from cannibalisation of a shallow water carbonate

Fig. 1. A, Position of the Dolodrook Inlier in the Mt Wellington Greenstone Belt on the eastern margin of the Melbourne Zone. B, Location of relevant limestone bodies in the Dolodrook River area. Base map: 1:25 000 topographic map Tali Karmg, 1st edn, 1990 (Viernap). Universal 1000 m grid reference are shown.

platform, deposited in a turbiditic environment, the Garvey Gully Formation. That trilobite faunas derived from the Dolodrook River limestones represent at least three distinct ages (see below) accords with a history of platform collapse, possibly episodic and triggered by tectonic events. It could also reflect the history of incision into deeper and older horizons on a now 'lost' carbonate platform. Because the limestone bodies of the Dolodrook River are an integral part of the Garvey Gully Formation and do not constitute a coherent stratigraphic unit within it, they are not accorded formal member status.

Of the eleven limestone outcrops sampled in the Dolodrook River area, only three seemingly fault-bounded lenses produced *Roanella platystrophioides* (Fig. 1B). The materials came from a sampled stratigraphic section on each body: D-RH, a 42.4 m section on the western flank of Roan Horse Gully commencing at 766₆417₅ on 1:25 000 topographic sheet Tali Karng; D-RHE, a 15 m section east of D-RH commencing at 770₂416₄; and, D-UCM, a 29.7 m section uphill southwards from the abandoned chromite mine commencing at 764₆413₉ (Fig. 1B).

The limestone on the western flank of Roan Horse Gully (D-RH; Fig 1B) is apparently fault-bounded on all sides; according to Duddy (1974) it has been thrust over Upper Ordovician slates. There is some uncertainty regarding facing of the limestone, but it is assumed to dip at 80°+ to the south, the presence of ultrabasics beneath the limestone according with younging to the south. There is apparently no development of the Garvey Gully Formation in this area; Duddy (1974) inferred that it had thinned or been faulted out.

Carbonate clasts up to 0.5 m across occur in a relatively coarse conglomeratic matrix about 200 m downstream along Roan Horse Gully from the presumed base of the limestone. The sequence appears to be part of the Mt Wellington Greenstone sequence but could be interpreted as anomalous Garvey Gully Formation represented by cannibalised ultramafics.

The petrology of the limestone in Roan Horse Gully has been commented upon briefly by Ebsworth (in Duddy 1974). The lower half of the limestone is dominated by algal pellets, with minor allochems consisting of trilobite debris, brachiopod shells and echinoderm ossicles. The original nature of the matrix is obscure, but now consists of recrystallised and/or dolomitised sparry calcite. The shells of *Roanella platystrophioides* are silicified in the lower half of the limestone. The upper half of the limestone tends to be massive, and contains few obvious bioclasts.

AGE OF THE DOLODROOK LIMESTONES

The trilobite faunas from the Dolodrook River limestones have never been formally described, though a species list was provided by Thomas & Singleton (1956); the whereabouts of the collections is presently unknown, presumed lost (D. J. Holloway, pers. comm.).

Dr Allison R. Palmer has provided one of us (GAB) with unpublished notes made during a re-evaluation of the Dolodrook trilobites on 13–14 April 1961, where the taxa listed by Thomas & Singleton (1956) were recognised by Palmer as a composite of at least 3 faunas. The oldest fauna, from limestone outcrops in Garvey Gully, is Middle Cambrian in age and represented by *Hypagnostus* (possibly 2 species), *Ptychagnostus australiensis* (Chapman), *Thielaspis thieli* (Chapman) (= *Mapania*?), a smooth agnostid and an indeterminate pychopariid. This is followed by an upper Mindyallan (*Crepicephalus* Zone equivalent) fauna consisting of *Crepicephalus etheridgei* (Chapman), *Bynumia*, *Cedaria* cf. *gaspensis*?, a new clanoaspid genus and species, *Aspidagnostus*?, an indeterminate corynexochid, and a solenopleurid with a *Bonnia*-like tail. The youngest fauna, which includes material from Roan Horse Gully exposures, is basal Idamean (*Aphelaspis* Zone equivalent) and includes *Agnostus inexpectans*, *Pseudagnostus* sp., *Olenaspella separata*, *Pseudagnostina*?, *Aspidagnostus laevis*?, *Corynexochus* cf. *plumula*, *Aphelaspis*?, *Proceratopyge*? and a smooth agnostid.

FAUNAL COMPOSITION AND DEPOSITIONAL ENVIRONMENT

The fauna in the lower half of the Roan Horse Gully Section D-RH is dominated almost entirely by *R. platystrophioides*. Using the seven criteria outlined by Levinton (1970: 77), and elaborated by Alexander (1977), *R. platystrophioides* could be considered an opportunistic species based on its restricted facies distribution, overwhelming faunal dominance, high density clustering, limited lateral distribution, and restricted stratigraphic occurrence. Alexander (1977) noted that the majority of opportunistic species are characterised by comparatively small biovolume, conservative deposition of calcium carbonate (leading to small size and shell thicknesses of less than 1.0 mm), and initially rapid growth rates leading to early sexual maturity—the last inferred from the distance between successive concentric growth lines. Though

R. platystrophioides has a comparable biovolume to the opportunistic species *Billingsella perfecta* from the Late Cambrian St Charles Formation of Utah and Idaho (Alexander 1977), and falls within the size range of a typical opportunist (mean maximum length 8–17 mm), it tends to have a thicker pedicle valve (up to 2 mm thick), and a greater degree of radial costellation than taxa identified by Alexander (1977) as opportunists. In addition, concentric growth lines tend to be lacking in *R. platystrophioides*, making it impossible to determine the growth rate of this species.

It is clear that, like *B. perfecta*, *R. platystrophioides* was attached to the substrate by a few pedicle threads as a juvenile (or subadult), but during subsequent growth the foramen was gradually closed (by deltidial plates in the case of *R. platystrophioides*); the shell is therefore inferred to have been free-lying at maturity. Given the extra weight and size of the pedicle valve it would seem reasonable to suggest that it must have been in contact with (or partially buried in) the substrate during life. Because of the high level of shell disarticulation (97%), abrasion and breakage, combined with the presence of oncolites, numerous algal pellets, and rare rounded lithic clasts we infer that *R. platystrophioides* inhabited a high energy, periodically storm influenced, near shore environment, presumably algal-bound tidal flats. The thick shell would have provided protection in such a hostile environment.

Other fossils recovered from D-RH include isolated pelmatozoan columnals, spongiomorph spicules, aphelaspis trilobites (Laurie, in prep.), a few unidentifiable lingulate brachiopod fragments, and a small, solitary, eup-shaped, coral-like organism of uncertain affinity. The D-UCM section produced fewer *R. platystrophioides* specimens than D-RH, but also produced pelmatozoan columnals and fragments of an indeterminate high spired gastropod. Only a few silicified *R. platystrophioides* were obtained from the relatively small D-RHE section. Algal pellets are common in the lower half of all three limestone tracts.

SYSTEMATIC PALAEOONTOLOGY

All figured specimens are in the Museum of Victoria; catalogue numbers are indicated in the figure captions.

Phylum BRACHIOPODA Dumeril 1806

Subphylum RHYNCHONELLIFORMEA
Williams et al. 1996

Class STROPHOMENATA Williams et al. 1996

Order STROPHOMENIDA Öpik 1934

Superfamily ?BILLINGSSELLOIDEA
Schuchert 1893

Family UNCERTAIN

Discussion. Despite being typically 'billingselloid' in overall appearance, the delthyrial cover in *Roanella* is a deltidium (or symphytium in mature specimens) formed by conjunct deltidial plates (Figs 2F, L, R; 3B, H). All known species of *Billingsella* are described as having a pseudodeltidium; Walcott (1912: 305) stated emphatically that 'no deltidial plates are known in the Billingsellidae'. The ontogenetic development of the delthyrial cover in *Roanella* begins with discrete deltidial plates (Fig. 2F, L), followed by gradual growth of a well developed deltidium with a median line of suture in subadult specimens (Fig. 3B, H), to development of a deltidium that has lost the median line of suture, forming a symphytium in mature specimens (Fig. 2R; Williams & Rowell 1965: H86). The symphytium strongly resembles a pseudodeltidium, but the presence of deltidial plates in a large number of specimens of *Roanella* cannot be confused with the ventrally restricted, convex pseudodeltidium, typically formed as a single plate during early embryonic growth in strophomenidine brachiopods (Arber 1942; Williams & Hewitt 1977).

Because the Class Strophomenata, as presently defined (Williams et al. 1996), includes only taxa with a pseudodeltidium (see also Brunton & Coeks 1996), the presence of a deltidium, could be taken as evidence for excluding *Roanella* from the Strophomenata. The presence of a deltidium in *Roanella* may be interpreted in two ways: either *Roanella* is an aberrant billingselloid taxon that for some reason, in geographic isolation, developed a deltidium instead of a pseudodeltidium, or *Roanella* represents a stock that displays remarkable convergence with billingselloid morphology. In support of the first view is the observation that, apart from the presence of a deltidium, *Roanella* is almost indistinguishable from taxa currently assigned to *Billingsella*. Wright (1996), among others, has noted that morphological characters may be fluid in 'the early phases of evolution of a group'; the presence of a deltidium in *Roanella* may thus represent a significant but not order-level divergence from the rest of the billingselloid clade. The presence of laminar secondary shell in *Roanella* would provide further evidence in support of billingselloid affinity (Williams 1970), but this

cannot be ascertained because silicification has obliterated the original secondary shell structure in all available material.

On the other hand, the presence of a deltidium in *Roanella* may be taxonomically significant at a high level, possibly reflecting a heritage far removed from the billingselloid clade. Given the widespread occurrence of convergence among invertebrate groups (Moore & Wilmer 1997) the close phenotypic similarity between *Roanella* and *Billingsella* may simply reflect adaptation to a similar suite of environmental parameters (especially relevant given that both taxa display numerous adaptations that allow them to survive in high energy, shallow water environments). Cladistic methodology tends to disguise possible examples of convergence (see detailed discussion in Moore & Wilmer 1997)—a point that should be kept in mind given that all recent supraordinal classifications of the Brachiopoda are based on cladistic analysis. Thus, identification of possible instances of convergence at the level of genus and species is notoriously difficult and is entirely dependent on accurate identification of phylogeny.

Wright & Rubel (1996) have noted the presence of a deltidium in the clitaubonitidine brachiopods; it is thus possible that *Roanella* may be an early member of this lineage. However, the clitaubonitidines are characterised by the presence of a spondylium (assumed to be formed by the fusion of dental plates), and Wright (1996: A63) has indicated that 'the clitaubonitidines must have arisen from an as yet unidentified late Cambrian orthocean stock with dental plates'. It should also be noted, nevertheless, that there is uncertainty regarding the origin of the spondylium in clitaubonitidines; Wright (1996: A63) has conceded that this structure may have evolved from a 'pseudospondylium formed from the thickening on the valve floor between the dental plates'. Despite the absence of dental plates in *Roanella*, there is consistent and prominent shell thickening in the umbonal region (often forming a prominent anterior boss; Fig. 3B, C, H, I), that may have been the precursor to an early spondylial structure.

What then can we conclude about the affinities of *Roanella*? If a billingselloid affinity is advocated, and the provisional placement of the Billingselloidea with the orthotetidine strophomenids by Williams et al. (1996) is accepted, then *Roanella* may be regarded as an aberrant strophomenoid with a deltidium. Williams et al. (1996: 1183) also placed the clitaubonitidines as a suborder in the Order Strophomenida and suggested that the deltidium in these brachiopods does not preclude assignment to the Class Strophomenata. *Roanella* can therefore also be viewed as a strophomenate brachiopod with a close affinity to the billingselloids. A deltidium has been reported previously in only a few early Palaeozoic orthoids, for example *Barbarorthis*, *Campylorthis* and *Tuvaella*, and though the possibility of convergence cannot be completely ruled out, the weight of morphological evidence indicates that *Roanella* is an unusual taxon exhibiting a combination of billingselloid and clitaubonitidine features. The presence of characters more typical of the billingselloid clade (such as the vascular system and brachial valve morphology) suggests *Roanella* should be assigned tentatively to the Billingselloidea, though the family-level assignment is left open.

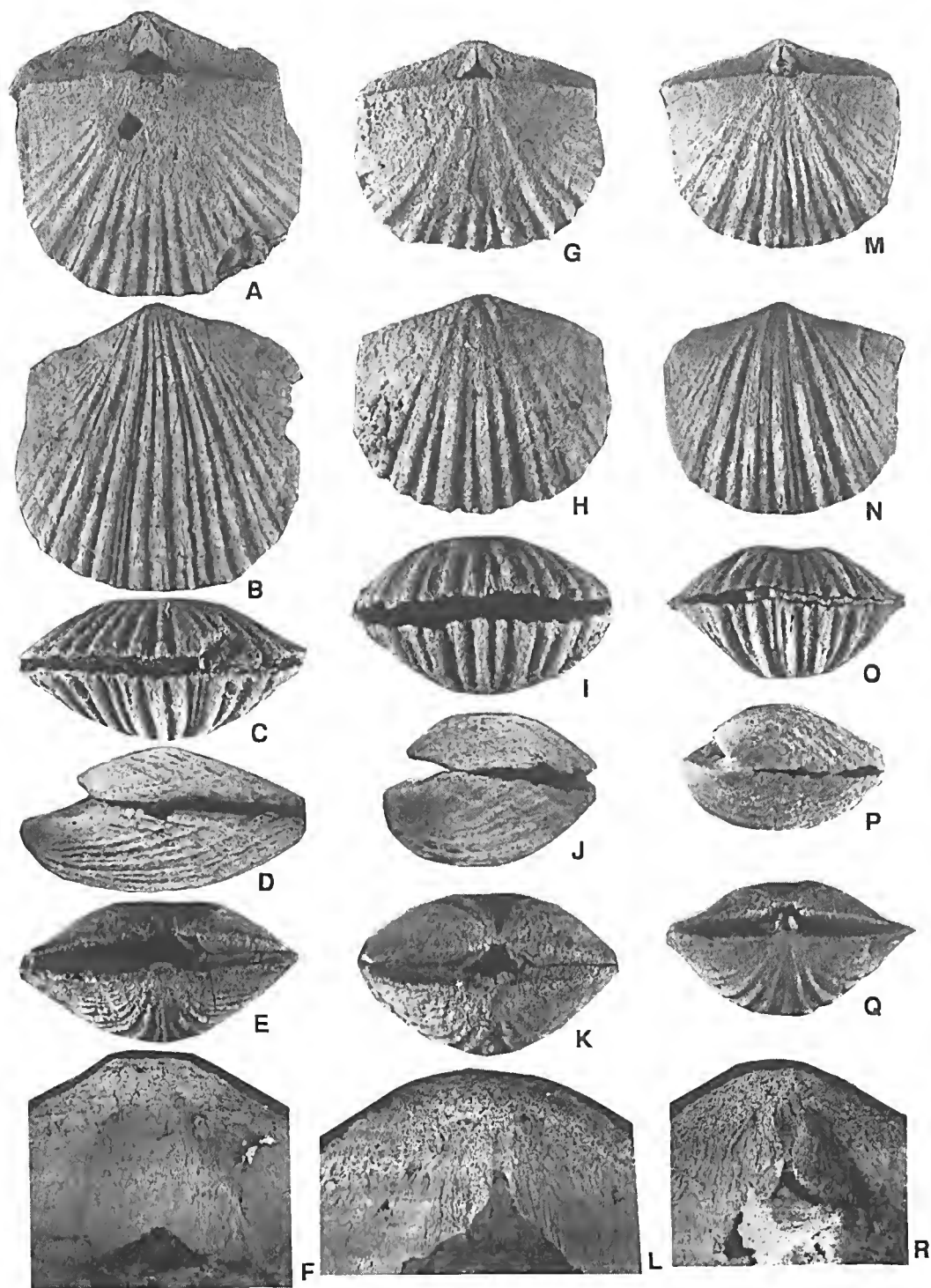
Roanella n. gen.

Type species. *Roanella platystrophioidea* (Chapman 1911: 311, pl. 59, figs 14, 15; pl. 60, fig. 24).

Etymology. After Roan Horse Gully, the type locality.

Diagnosis. Small (maximum width 17 mm), ventri-biconvex, unequally costellate shell with semi-circular to subquadrate outline. Pedicle valve thick-shelled, mostly with sharply alate hingeline; delthyrial cover formed by coalescence of deltidial plates to form a deltidium or symphytium; teeth small, poorly defined, lacking dental plates; ventral muscle field deeply impressed with raised median boss defining anterior margin of field, mantle canal system saccate. Brachial valve lacking chilidium.

Fig. 2. Articulated specimens of *Roanella platystrophioidea* (Chapman). All specimens from D-RH 21.7. A-E, Dorsal, ventral, anterior, lateral and posterior views of NMV P148697, $\times 3.5$. F, Enlargement of symphytium of NMV P148697, $\times 15$. G-K, Dorsal, ventral, anterior, lateral and posterior views of NMV P148698, $\times 6$. L, Enlargement showing disjunct deltidial plates of NMV P148698, $\times 16$. M-Q, Dorsal, ventral, anterior, lateral and posterior views of NMV P148699, $\times 6$. R, Enlargement showing disjunct deltidial plates of NMV P148699, $\times 22$.



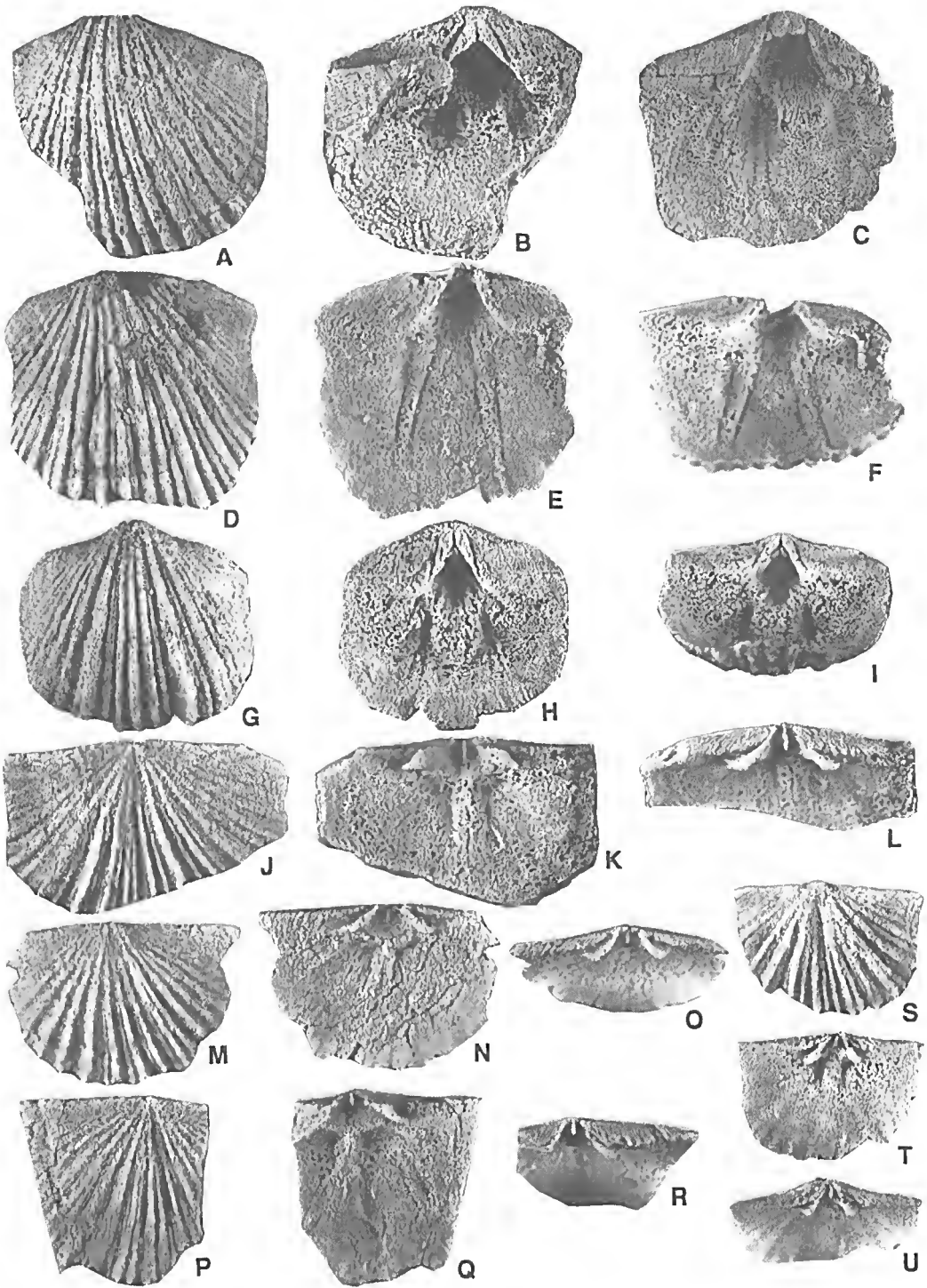
Discussion. The distinction between deltidial plates and lateral plates is not immediately apparent, though the latter term has rarely been used in descriptions by more recent workers. Schuchert & Cooper (1932: 22–23) reported the development of 'lateral plates' overlapping a 'stiffened' pseudo-deltidium in some orthoids (eg. *Hesperorthis*), and though the umbo of *Roanella* is filled with thickened deposits of secondary shell material (similar to *Billingsella*) under the deltidium, this should not be confused with a true pseudo-deltidium (see Arber 1942). Schuchert & Cooper (1932) stated that 'lateral plates' never join in the median plane and can thus be distinguished from deltidial plates, but the two are here regarded as essentially synonymous. The deltidium in *Roanella* is also comparable to the so-called notodeltidium in the Middle Devonian genus *Phragmophora* described and illustrated by Cooper (1955: 52, pl. 14A, figs 1–7). However, the notodeltidium completely fills the delthyrium in *Phragmophora* (Williams & Rowell 1965: H148) whereas in *Roanella* the deltidium occupies only the apical $\frac{1}{2}$ – $\frac{1}{3}$ of the delthyrium (Figs 2A, F, G, L, M, R; 3B, H), and eventually seals the foramen.

Roanella can be distinguished from *Billingsella* by the presence of a deltidium in the former; this feature alone is probably significant enough to warrant erection of a new billingselloid family based on *Roanella*, though brachial valves of the two genera are essentially indistinguishable (see Fig. 3J–U). It should be noted that evidence is mounting to suggest that *Billingsella* is probably an amalgam of at least two (possibly more) genera. The concept of the genus *Billingsella* has been detailed by various authors (Walcott 1905: 227, 1912: 749; Schuchert & Cooper 1932: 48–49; Ulrich & Cooper 1938: 72; Bell 1941: 245; Nikitin 1956: 24; Williams & Wright 1965: H305; Freeman & Stitt 1996: 359). Many workers have documented the substantial morphological plasticity of *Billingsella* (eg. Schuchert & Cooper 1932; Bell 1941; Bell & Ellinwood 1962; Mackinnon, in

Shergold et al. 1976; Freeman & Stitt 1996) noting the variable development of radial ornament, dental plates, cardinal process, chilidium, vascular markings and apical foramen. Laurie (1997), for example, has noted the fundamental difference between the mantle canal patterns exhibited by *B. plicatella* Walcott which has a digitate mantle canal system in the brachial valve and a saccate mantle canal system in the pedicle valve (see Bell 1941: pl. 34, figs 4–12; Williams & Wright 1965: fig. 135g), and *B. perfecta* which is characterised by a digitate mantle canal system in the pedicle valve. Such differences in vascular markings have recently been used to discriminate new genera of closely related orthoids (Jaanusson & Bassett 1993) and elitambonitidines (Wright & Rubel 1996). In addition, the lack of dental plates in all published species assigned to *Billingsella* from the Southern Hemisphere contrasts significantly with the development of prominent dental plates in most North American species, including the type species (see Schuchert & Cooper 1932: 28). The occasional description of a symphytium in *Billingsella* (eg. Cowen 1969) also raises the possibility that some specimens may, in fact, be related to *Roanella*. Though it is clearly beyond the scope of the present paper to review all taxa currently assigned to *Billingsella*, such a revision could potentially distinguish new taxa and help clarify early evolutionary trends within the Billingselloidea, a clade which is currently thought to be the stem group of the Class Strophomenata (Williams et al. 1996: fig. 6).

Roanella, in common with the billingselloid genera *Cymbithyrus* Cooper 1952 and *Xenorthis* Ulrich & Cooper 1938 lacks dental plates, but *Cymbithyrus* has a concavo-convex shell (Cooper 1952: 5, pl. 1B, 16, 20), and *Xenorthis* has a distinctly uniplicate commissure. *Saccogomum* Havlicek 1971 has a finer, multicostellate ornament and shorter vaseula media than *Roanella* (see Cornée et al. 1987: 521–522, pl. 1A–D). Mergl et al. (1998) also report the presence of a pseudo-

Fig. 3. Pedicle and brachial valves of *Roanella platystrophioidea* (Chapman). All specimens from D-RH 21.7 with magnification $\times 3.5$. A–B, Exterior and interior of pedicle valve NMV P148700 (note presence of disjunct deltidial plates and billingselloid-like vascular markings). C, Interior of NMV P148701. D–F, Exterior, interior and oblique interior of NMV P148702 with strong vaseula media (note deltidial plates broken away in this specimen). G–I, Exterior, interior and oblique interior of NMV P148703 with more rounded outline and deep umbonal cavity bordered anteriorly by well developed median boss. J–L, Exterior, interior and posterior of NMV P148704 (note blade-like cardinal process and short median ridge). M–O, Exterior, interior and posterior of NMV P148705. P–R, Exterior, interior and posterior of NMV P148706. S–U, Exterior, interior and posterior of juvenile specimen, NMV P148707.



deltidium and short dental plates in species of *Saccogonum* from Morocco. The poorly known *Eosotrematorthis* Wang from the Arenig of northern China (Wang 1955) is apparently more strongly costellate than *Roanella* (see Williams & Wright 1965: H306). *Ocnorthis* Bell 1941 is also similar to *Roanella*, especially in juvenile stages, but can be distinguished by its open delthyrium and elevated dorsal median ridge (Bell 1941: 252).

Roanella platystrophioides (Chapman)

Figs 2A–R; 3A–U

Platystrophia biforata (Schlotheim 1820); Chapman 1907: 34.

Orthis (*Plectorthis*) *platystrophioides* Chapman 1911: 311, pl. 59, figs 14, 15; pl. 60, fig. 24.

?*Eoorthis platystrophioides* Chapman 1917: 96.

Material. Chapman (1911) did not designate a holotype from his collections. His illustrated specimens (syntypes NVM P12312–P12315; Chapman 1911: pl. 59, figs 14–15; pl. 60, fig. 24) are poorly preserved and display only external morphology. Specimen NVM P12314 a ventral valve, illustrated by Chapman (1911: pl. 60, fig. 24—centre specimen on bottom row) is here designated as the lectotype. Specimens NVM P12312, NVM P12313 and NVM P12315 become paralectotypes. No information on internal morphology or the delthyrial cover can be ascertained from this type material making it impossible to adequately clarify taxonomic relationships. However, the material derived from the type locality in Roan Horse Gully by the authors is represented by abundant, well preserved silicified shells detailing internal and external morphology and ontogeny. Eleven specimens (NMV P148697–P148707) are illustrated herein. The collections also contain 371 brachial valves (NMV P148708), 1519 pedicle valves (NMV P148709) and 34 complete shells (NVM P148710) from the type locality, D-RH/21.7. In addition, 74 brachial valves (NVM P148711), 160 pedicle valves (NVM P148712), and 28 complete shells (NVM P148713) come from D-UCM/10 and 3 brachial valves (NVM P148714) and 44 pedicle valves (NVM P148715) from D-UCM/13.8.

Type locality. Limestone tract outcropping on the western flank of Roan Horse Gully at 766.4175 on the 1:25 000 topographic sheet Tali Karng (see Fig. 1B).

Diagnosis. As for genus.

Description. Shell small (maximum width 17 mm), dominantly ventribiconvex, semicircular to subquadrate in outline; maximum shell width generally at hingeline in alate specimens, and at midlength in some non-alate specimens; anterior commissure rectimarginate to faintly sulcate; radial ornament unequally costellate, consisting of 7–12 rounded

primary costellae, with thinner, secondary costellae arising primarily by intercalation; growth lamellae not preserved.

Pedicle valve up to 2 mm thick. Interarea wide and long, flat or gently concave in profile, triangular and apsacline, cleft medianly by a wide, V-shaped delthyrium subtending an angle of 60–70°; deltidium or symphytium arched, covering apical $\frac{1}{3}$ – $\frac{1}{2}$ of delthyrium; foramen poorly defined, tiny or completely lacking (overgrown); teeth simple, small, blunt, lacking dental plates; ventral muscle field large, deeply impressed, occupying entire floor of umbonal chamber, extending up to 50% shell length, with anterior margin raised and thickened by secondary shell to form a pronounced rounded boss; Mantle canal system saccate, vascula media strongly impressed, arcuate, originate either side of the boss at the anterior margin of the ventral muscle field, extending approximately 80% shell length, then (in one specimen) curving posterolaterally to become parallel with the valve margin.

Brachial valve with well defined, long, narrow, anacline interarea; notothyrium open; chilidium lacking. Notothyrial cavity with well developed, raised platform bisected medianly by simple, narrow, ridge-like cardinal process; sockets large, deep and cylindrical, excavated into posterior shell wall, but partly floored in some specimens by small 'fulcral' plates. Socket ridges short, massive, tusk-like; median ridge short, wide, low, occurring under, and anterior to the notothyrial platform, and merging imperceptibly with the shell floor; musculature and mantle canal system unknown.

Ontogeny. Large numbers of individuals from Roan Horse Gully show that smaller shells (<5 mm) tend to be weakly equibiconvex with a shallow, but distinct median sulcus on the brachial valve; the shell outline also tends to be more rounded and equidimensional. As the shell increases in size the outline tends to become more subquadrate and the shell more transverse. The pedicle valve becomes thicker and deeper, giving the shell a ventribiconvex lateral profile. The sulcus in the brachial valve gradually becomes weaker until it is almost imperceptible. At no stage during growth is a fold developed on the pedicle valve, though larger specimens sometimes develop a faintly sulcate commissure.

Discussion. Chapman (1907) originally misidentified this taxon as the species *Platystrophia biforata* (Schlotheim, 1820), based on comparison with shells also misidentified as *P. biforata* from the allochthonous Early Devonian limestones at Deep

Creek, east of Walhalla, Victoria. However, after the discovery of Upper Cambrian trilobites in limestones from the Dolodrook River, the taxon was redescribed by Chapman (1911) as *Orthis* (*Plectorthis*) *platystrophioides* n. sp. The limited number of specimens upon which Chapman (1911) based his description are in poor condition, consisting entirely of articulated specimens mechanically 'cracked out' of limestone. No description of the interior of this species was provided by Chapman (1911). Recovery of large numbers of well preserved silicified specimens from the Roan Horse Gully locality from which Chapman's material came has provided an opportunity for re-evaluation of the systematic position of this form.

Chapman's assignment of this form to *Orthis* (*Plectorthis*) was undoubtedly based on the biconvex, strongly costellate nature of the shells and the belief that it had a large open delthyrium (Chapman 1911: 311). He also noted the presence of an incurved beak and median fold on the pedicle valve. None of the 1733 silicified pedicle valves in the current collections display any evidence of a median fold or an incurved beak (see for example Fig. 2D, J, P). Chapman (1917) later transferred this species to *Eoorthis* based on specimens collected from the Knowsley East Formation at Heathcote, but did not illustrate the material or explain the reason for re-assignment to *Eoorthis*.

R. platystrophioides generally lacks a functional foramen; in this respect it is similar to many species of *Billingsella* (Frecman & Stitt 1996). In the few specimens with a foramen, it is so tiny that it is difficult to envisage it as a conduit for a functional pedicle. Ulrich & Cooper (1938: 72) commented upon the unusually small size of the foramen in *Billingsella* and hypothesised that the 'pedicle must have been a mere thread or perhaps a bundle of threads which serve to attach the animal to floating objects or possibly to the bottom'. That many species of *Billingsella* occur as monospecific populations, often associated with sedimentary structures indicative of shallow, turbulent environments (eg. oncolites) does not accord with a floating lifestyle. Ulrich & Cooper (1938: 72) noted that a similar sealing up of the foramen occurred in the elitambonitid species *Estlandia* and *Clitambonites*.

R. platystrophioides can be distinguished from the bulk of *Billingsella* species described from the Middle and Upper Cambrian of North America, such as *B. pepina* (Hall), *B. perfecta* Ulrich & Cooper, *B. coloradoensis* (Shumard), *B. rectangulata* Cooper and *B. corrugata* Ulrich &

Cooper by its coarser costellate ornament, lack of concentric growth lamellae and, more importantly, the presence of a deltidium and lack of dental plates (Fig. 3F, I). Dental plates are well developed in most North American *Billingsella* species, eg. *B. perfecta* (Ulrich & Cooper 1938: pl. 7, figs 11, 20–21; Bell 1941: pl. 35, figs 1, 4–5, 10–14), and *B. rectangulata* (Cooper 1952: pl. 1, figs 11, 13–15). Nikitin (1956) described several *Billingsella* species from the Cambrian of Kazakhstan, but most exhibit finer costellation than *R. platystrophioides*, or are significantly larger in size. *B. destombesi* from the Middle Cambrian of Morocco (Mergl 1983: 338, pl. 1, figs 13–16) is larger than *R. platystrophioides*, and can be distinguished by its strong, short, dental plates, finer radial costellae and longer median ridge in the brachial valve.

The few species of *Billingsella* previously described from the Southern Hemisphere are based on limited and/or poorly preserved material (often tectonised moulds in shales), making comparison with *Roanella* difficult. Percival (in Powell et al. 1982: 147–148, fig. 12, 1–5) described *Billingsella* sp. from the Upper Cambrian (Idamean) Cupala Creek Formation in western NSW and, despite the limited material and preservation as internal moulds, this species can be distinguished from *R. platystrophioides* on the basis of its dorsi-biconvex shell, finely multicostellate ornament and 'prominent widely-spaced concentric growth lamellae'. The *Billingsella* species from the Cupala Creek Formation is probably conspecific with *Billingsella* sp. indet. of Mackinnon (in Shergold et al. 1976: pl. 38, figs 11–19) from the Middle–Late Cambrian Mariner Formation, Northern Victoria Land, Antarctica (Percival, in Powell et al. 1982; Rowell, in Henderson et al. 1992). Mackinnon (in Shergold et al. 1976: pl. 38, figs 17–18) recovered a juvenile brachial valve of this species with a strongly developed median ridge extending to the anterior margin of the valve. A comparable ridge does not occur in brachial valves of *R. platystrophioides* of similar size.

Billingsella sp. 1 of Jago (1989: 40, pl. 2, figs A–J) from the early Late Cambrian (Idamean) Singing Creek Formation, Deniston Range, south-western Tasmania, can be distinguished only on external features, there being little information on interior structure. It has a subtrapeziform shell, fine parvicostellate radial ornament, and a pedicle valve with a low median fold and 'slightly concave posterolateral slopes' (Jago 1989: 40).

The taxon closest to *R. platystrophioides* is *B. cf. borukaevi* described by Rowell (in Henderson et al. 1992: 256, pl. 4, figs 1–5) from the early

Late Cambrian (Idamean) Minaret Formation, Ellsworth Mountains, West Antarctica. The shell dimensions, convexity, outline and radial ornament are indistinguishable from *R. platystrophioides*, even to the extent that Rowell (in Henderson 1992: 256) describes similar variation in the position of the maximum shell width, depending on the auriculate nature of the hingeline. Rowell (in Henderson et al. 1992) describes the presence of a pseudodeltidium in *B. cf. borukaevi* but, given the indifferent preservation and the limited material, it is possible that a symphytium rather than a pseudodeltidium is present. Unfortunately, the interior of the pedicle valve is not known in *B. cf. borukaevi* so no information is available on the dental plates nor the configuration of the muscle field and vascular system. However, *B. cf. borukaevi* can be distinguished from *R. platystrophioides* by the development of a 'broad conspicuous [median] ridge' extending 'to near the midlength of the valve' in the brachial valve of the former (Rowell, in Henderson et al. 1992: pl. 4, fig. 1). In contrast, the median ridge in the brachial valve of *R. platystrophioides* is merely a buttress under the notothyrial platform, and extends less than $\frac{1}{3}$ shell length (Fig. 3K, N, Q, T). *B. borukaevi*, originally described by Nikitin (1956: 30–31, pl. 2, figs 1–20), can be distinguished from *R. platystrophioides* by its dorsibiconvex profile and flatter pedicle valve.

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REFERENCES

- ALEXANDER, R. R., 1977. Growth, morphology and ecology of Paleozoic and Mesozoic opportunistic species of brachiopods from Idaho–Utah. *Journal of Paleontology* 51: 1133–1149.
- ARBER, M. A., 1942. The pseudodeltidium of the strophomenid brachiopods. *Geological Magazine* 79: 179–187.
- BELL, C. W., 1941. Cambrian Brachiopoda from Montana. *Journal of Paleontology* 15: 193–255.
- BELL, C. W. & ELLINWOOD, H. L., 1962. Upper Franconian and Lower Trempealeauan Cambrian trilobites and brachiopods, Wilberns Formation, Central Texas. *Journal of Paleontology* 36: 385–423.
- BRUNTON, C. H. C. & COCKS, L. R. M., 1996. The classification of the brachiopod order Strophomenida. In *Brachiopods*, P. Copper & J. Jisuo, eds, Balkema, Rotterdam, 47–51.
- CAS, R. A. F., 1983. A review of the palaeogeographic and tectonic development of the Lachlan Fold Belt of southeastern Australia. *Geological Society of Australia, Special Publication* 10: 1–104.
- CHAPMAN, F., 1904. On some brachiopods and a bivalve from Heathcote. *Records of the Geological Survey of Victoria* 1: 222–226.
- CHAPMAN, F., 1907. On some fossils from Silurian limestones, Dolodrook Valley, Mt Wellington, Victoria. *Victorian Naturalist* 24: 34–35.
- CHAPMAN, F., 1908. Preliminary notes on a collection of trilobite remains from the Dolodrook River, N. Gippsland. *Proceedings of the Royal Society of Victoria* 21: 268–269.
- CHAPMAN, F., 1911. On a trilobite fauna of Upper Cambrian age (*Olenus* Series) in N.E. Gippsland, Victoria. New or little known Victorian fossils in the National Museum, Pt 12. *Proceedings of the Royal Society of Victoria* 23: 305–323, pls 59–61.
- CHAPMAN, F., 1917. The Heathcote Fauna. *Records of the Geological Survey of Victoria* 4: 89–102, pls 6–7.
- CHAPMAN, F. & THOMAS, D. E., 1936. The Cambrian Hydroids of the Heathcote and Monegetta districts. *Proceedings of the Royal Society of Victoria* 48: 193–219.
- COLLINS, W. J. & VERNON, R. H., 1994. A rift–drift–delamination model of continental evolution: Palaeozoic tectonic developments of eastern Australia. *Tectonophysics* 235: 249–275.
- COOPER, G. A., 1952. New and unusual species of brachiopods from the Arbuckle Group in Oklahoma. *Smithsonian Miscellaneous Collections* 117: 1–35, pls 1–4.
- COOPER, G. A., 1955. New genera of Middle Paleozoic brachiopods. *Journal of Paleontology* 29: 45–63.
- CORNEE, J. J., TAYEBI, M. & HAVLICEK, V., 1987. Découverte de *Saccogonum* cf. *saccatum*, brachiopode du Cambrien (Supérieur ?), dans le Haut-Atlas Occidental (Maroc). Conséquences stratigraphiques et structurales. *Geobios* 20: 517–527.
- COWEN, R., 1969. Stegidal structures in spiriferide brachiopods. *Journal of Paleontology* 43: 538–539.
- CRAWFORD, A. J., 1988. Cambrian. In *Geology of Victoria*, J. G. Douglas & J. A. Ferguson, eds, Geological Society of Australia, Victorian Division, 37–62.
- CRAWFORD, A. J. & BERRY, R. F., 1992. Tectonic implications of Late Proterozoic–Early Palaeozoic igneous rock associations in western Tasmania. *Tectonophysics* 214: 37–56.

- CRAWFORD, A. J., CAMERON, W. E. & KEAYS, R. R., 1984. The association boninite-low Ti andsite-tholeiite in the Heathcote Greenstone Belt, Victoria: ensimatic setting for the early Lachlan Foldbelt. *Australian Journal of Earth Sciences* 31: 161-175.
- CRAWFORD, A. J. & KEAYS, R. R., 1978. Petrogenesis of Victorian Cambrian tholeiites and implications for the origin of associated boninites. *Journal of Petrology* 28: 1075-1109.
- DUDDY, I. R., 1974. *The Geology of the Dolodrook River Lower Palaeozoic inlier and Petrological studies of Cambrian rocks*. Unpublished Honours Thesis, Department of Geology, University of Melbourne.
- ETHERIDGE JR, R., 1896. Evidence of a Cambrian fauna in Victoria. *Proceedings of the Royal Society of Victoria* 8: 52-64.
- FREEMAN, R. J. & STITT, J. H., 1996. Upper Cambrian and lowest Ordovician articulate brachiopods from the Arbuckle and Wichita Mountains, Oklahoma. *Journal of Paleontology* 70: 355-372.
- GLEN, R. A., 1992. Thrust, extensional and strike-slip tectonics in an evolving Palaeozoic orogen—a structural synthesis of the Lachlan Orogen of southeastern Australia. *Tectonophysics* 214: 341-380.
- GREGORY, J. W., 1903. The Heathcoteian, a pre-Ordovician series, and its distribution in Victoria. *Proceedings of the Royal Society of Victoria* 15: 148-175, pls 23-26.
- HARRIS, W. J. & THOMAS, D. E., 1954. Notes on the geology of the Wellington-Macalister area. *Mining and Geological Journal* 5: 34-47.
- HENDERSON, R. A., DEBRENNE, F., ROWELL, A. J. & WEBERS, G. F., 1992. Brachiopods, archaeocyathids, and Pelmatozoa from the Minaret Formation of the Ellsworth Mountains, West Antarctica. *Geological Society of America, Memoir* 170: 249-267.
- HOWITT, A. M., 1891. Notes on Lake Karng. *Quarterly Report of the Mining Department, Victoria* September 1891: 26.
- JAANUSSON, V. & BASSETT, M. G., 1993. *Orthambonites* and related Ordovician brachiopod genera. *Palaeontology* 36: 21-63.
- JAGO, J. B., 1989. Late Cambrian brachiopods from the Denison Range, southwestern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 123: 37-42.
- LAURIE, J. R., 1997. Silicified Late Cambrian brachiopods from the Georgina Basin, western Queensland. *Alcheringa* 21: 161-171.
- LEVINTON, J. S., 1970. The paleoecological significance of opportunistic species. *Lethaia* 3: 69-78.
- MERGL, M., 1983. New brachiopods (Cambrian-Ordovician) from Algeria and Morocco (Mediterranean Province). *Casopis pro Mineralogii a Geologii* 28: 337-349.
- MERGL, M., GEYER, G. & EL ATTARI, A., 1998. The billingsellid genus *Saccogonum* (Brachiopoda) from the Moroccan Cambrian and its significance for the regional geology and stratigraphy. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 209: 273-293.
- MOORE, J. & WILLMER, P., 1997. Convergent evolution in invertebrates. *Biological Review* 72: 1-60.
- MURRAY, R. A. F., 1879. Geological sketch map No. 2 S.E. Gippsland. *Geological Survey of Victoria, Progress Report* 5: 44-70.
- NELSON, D. R., CRAWFORD, A. J. & MCCULLOCH, M. T., 1984. Nd-Sr isotopic and geochemical systematics in Cambrian boninites and tholeiites from Victoria, Australia. *Contributions to Mineralogy and Petrology* 88: 164-172.
- NIKITIN, I. F., 1956. *Brachiopody kembriya i nizhnego ordovika severo-vostoka Tsentral'nogo Kazakhstana*, 143 pp., 15 pls. Akademiya Nauk Kazakhskoy SSR, Alma-Ata. [In Russian.]
- ÖPK, A. A., 1949. A Middle Cambrian trilobite from Victoria—*Centroporella neglecta* n. sp. *Mining and Geological Journal Victoria* 3: 55-58.
- POWELL, C. MCA., NEEF, G., CRANE, D., JELL, P. A. & PERCIVAL, I. G., 1982. Significance of Late Cambrian (Idamean) fossils in the Cupala Creek Formation, northwestern New South Wales. *Proceedings of the Linnean Society of NSW* 106: 127-150.
- SCHUCHERT, C. & COOPER, G. A., 1932. Brachiopod genera of the suborders Orthoidea and Pentamerioidea. *Memoirs of the Peabody Museum of Natural History* 4: 1-270.
- SCHLOTHEIM, E. F. VON, 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung einer Sammlung versteinerter und fossiler Überreste der Tier- und Pflanzenreichs der Vorwelt erläutert*, vol. 1: 1-378. Gotha.
- SHERGOLD, J. H., COOPER, R. A., MACKINNON, D. I. & YOCHELSON, E. L., 1976. Late Cambrian Brachiopoda, Mollusca, and Trilobita from Northern Victoria Land, Antarctica. *Palaeontology* 19: 247-291.
- TEALE, E. O., 1920. A contribution to the Palaeozoic geology of Victoria, with special reference to the districts of Mount Wellington and Nowa Nowa, respectively. *Proceedings of the Royal Society of Victoria* 32: 67-146.
- THIELE, E. O., 1905. A trip to Lake Karng and Mount Wellington, north Gippsland. *The Victorian Naturalist* 22: 22-30.
- THIELE, E. O., 1906. Notes on the upper Macalister Valley, north Gippsland. *The Victorian Naturalist* 23: 8-18.
- THIELE, E. O., 1907. Physiographical and geological notes on the Mt Wellington district, north Gippsland. *The Victorian Naturalist* 24: 22-35.
- THIELE, E. O., 1908. Notes on the Dolodrook Serpentine area and the Mt Wellington rhyolites, north Gippsland. *Proceedings of the Royal Society of Victoria* 21: 249-267.
- THOMAS, D. E. & SINGLETON, O. P., 1956. The Cambrian stratigraphy of Victoria. In *El Sistema Cambrico, su paleogeografia y el problema de su base*, J. Rodgers, ed., Report of the 20th International 20th Geological Congress, Mexico, 2: 149-163.

- ULRICH, E. O. & COOPER, G. A., 1938. Ozarkian and Canadian brachiopoda. *Geological Society of America, Special Papers* 13: 1-321.
- VANDENBERG, A. H. M., 1988. Palaeozoic stratigraphy of Victoria. In *Victorian Geology Excursion Guide*, I. Clark, B. Cook & G. C. Cochrane, eds, pp. 15-38. Australian Academy of Science, and Geological Society of Australia (Victorian Division).
- WALCOTT, C. D., 1905. Cambrian Brachiopoda with descriptions of new genera and species. *Proceedings of the US National Museum* 28: 227-337.
- WALCOTT, C. D., 1912. Cambrian Brachiopoda. *US Geological Survey Monograph* 51: 872 pp., 104 pls.
- WANG, Y., 1955. New genera of brachiopods. *Academia Sinica, Scientia Sinica* 4: 327-357.
- WILLIAMS, A., 1970. Origin of laminar-shelled articulate brachiopods. *Lethaia* 3: 329-342.
- WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. & POPOV, L., 1996. A supraordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London Series B*, 351: 1171-1193.
- WILLIAMS, A. & HEWITT, R. A., 1977. The delthyrial covers of some living brachiopods. *Proceedings of the Royal Society, London B* 197: 105-129.
- WILLIAMS, A. & ROWELL, A. J., 1965. Morphology. In *Treatise on Invertebrate Paleontology*, R. C. Moore, ed., Part H, Brachiopoda 1, pp. H57-H138. Geological Society of America and University of Kansas Press, Lawrence.
- WILLIAMS, A. & WRIGHT, A. D., 1965. Orthida. In *Treatise on Invertebrate Paleontology*, R. C. Moore, ed., Part H, Brachiopoda 1, pp. H299-H359. Geological Society of America and University of Kansas Press, Lawrence.
- WRIGHT, A. D., 1996. Some morphological problems of brachiopod taxonomy. *GFF* 118: A62-A63.
- WRIGHT, A. D. & RUBEL, M., 1996. A review of the morphological features affecting the classification of clitambonitidine brachiopods. *Palacontology* 39: 53-75.

THE KANGAROOS OF YAN YEAN: HISTORY OF A PROBLEM POPULATION

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The catchment of Yan Yean Reservoir is situated on the rural fringe of Melbourne, southeastern Australia, and supports a large population of eastern grey kangaroos (*Macropus giganteus* Shaw). Yan Yean has a mean annual rainfall of 667 mm, which is distributed evenly throughout the year. Eight prominent eucalypt associations occur in the catchment and a total of 310 plant species have been recorded, including a number of threatened taxa as well as invasive weeds. Yan Yean also has a rich vertebrate fauna: 37 mammal, 155 bird, 28 reptile and 18 amphibian species. We have distinguished five habitat zones in the catchment and adjacent farmland, each reflecting a different land-use history. The first human inhabitants, the Wurunjerri-baluk people, were displaced initially by European settlers who began to log, graze and crop the area in the 1830s, and then by construction of the Yan Yean Reservoir in the 1880s. The catchment is closed to the public. Despite the construction of a kangaroo-proof fence, kangaroos have been a source of problems within the catchment and surrounding agricultural land for five decades. The population has been the focus of research into a number of aspects of ecology, particularly population dynamics, demography and parasitology. Despite a variety of techniques used and areas covered, previous surveys of population size have returned estimates ranging between 1770 and 3000 kangaroos, with little evidence of change since the 1960s.

Key words: Yan Yean, eastern grey kangaroo, *Macropus giganteus*, vegetation, vertebrates, Wurunjerri, European settlement, reservoir, kangaroo culling, kangaroo ecology, population survey.

THE eastern grey kangaroo (*Macropus giganteus* Shaw) is common through much of its range on the slopes of the Great Dividing Range and on the semi-arid plains of eastern Australia (Poole 1982). The species occurs in open forest, woodlands and grassland margins, favouring habitats with lateral cover offered by trees or shrubs, together with suitable forage provided by grasses in the ground layer (Caughley 1964; Bell 1973; Hill 1981; Taylor 1985a; Southwell 1987).

Eastern grey kangaroos can become over-abundant in rural settings where patches of woodland or forest are adjacent to improved pastures or crops (Taylor 1984, 1985b; Hill et al. 1988). Farmers often view them as pests that compete with domestic stock for pasture and water, and cause damage to fences and crops (Dempster 1961; Lavery & Kirkpatrick 1985). Over-abundant populations also arise in nature reserves where remnant native forest, woodland or shrubland abut former pasture, as occurs at Rotamah Island in The Lakes National Park, Victoria (Coulson &

Raines 1985) and Tidbinbilla Nature Reserve in the Australian Capital Territory (Neave & Tanton 1989).

The kangaroos of Yan Yean Reservoir Catchment illustrate these trends. The catchment forms a mosaic of significant remnants of native woodlands and shrublands, in combination with grassy clearings, forming highly productive habitat for eastern grey kangaroos. This system lies within a matrix of farmland, which is also exploited by the kangaroos. The purpose of this paper is to provide a background for a multi-disciplinary study, which began in 1992, into the ecology and management of the kangaroo population in this valuable research environment.

STUDY AREA

Yan Yean Reservoir Catchment (145°09'E, 37°32'S) is situated approximately 37 km northeast of Melbourne, Victoria, Australia (Fig. 1). The catchment

is 2250 ha in area. It is part of the Nillumbik Terrain, a basin to the north and east of Melbourne which contains the Plenty River, Yarra River,

Diamond Creek, Merri Creek, Darebin Creek and their tributaries. The catchment of Yan Yan is an area of undulating hills which are an extension of

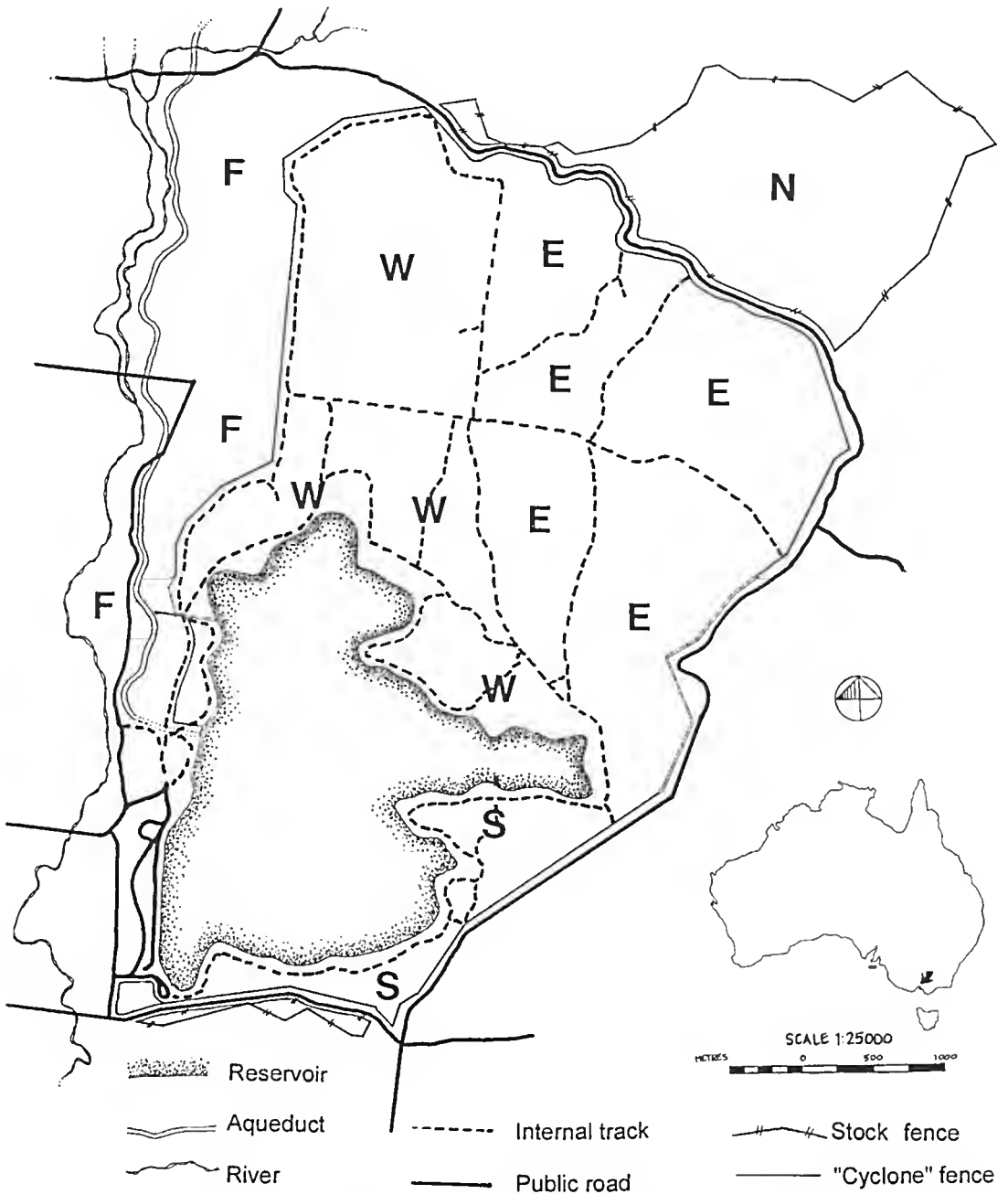


Fig. 1. Map of the study site at Yan Yan Reservoir Catchment, showing the five habitat zones (N=North; S=South; E=East; W=West; F=Farmland). Inset shows the location of Yan Yan in Victoria, Australia.

denuded ridges descending southwards from the Kinglake Plateau. The catchment has the primary role of production and storage of water as part of the supply to the Greater Melbourne area, and is managed by Melbourne Water. The reservoir has a capacity of 30 000 ML, and has a surface area of 560 ha when filled to capacity at 185 m above sea level (MMBW 1989).

Yan Yean is mostly surrounded by farmland, which is being increasingly subdivided for hobby farms and residential blocks. The northeast corner of the catchment abuts the township of Whittlesea (population 2500). Much of the study area is enclosed by a 1.8-m 'Cyclone' chain-mesh security fence topped with three strands of barbed wire. The security fence forms only a partial barrier to kangaroos, which have forced the mesh up from the base and established well-worn runways in many places. Public roads run beside this fence along the northern, eastern and southern boundaries of the catchment, and along part of the western side (Fig. 1). The catchment is closed to the public, and has a network of unsealed roads maintained for management purposes.

Climate

Daily rainfall data have been collected at Yan Yean since September 1855. Yan Yean has a temperate climate, with a mean annual rainfall of 667 mm. The wettest year was 1872, when 1048 mm of rain was recorded; the driest was 1945 when only

370 mm of rain fell. There is little difference in mean monthly precipitation throughout the year (Fig. 2). February has the lowest and most variable rainfall (mean \pm s.d. = 45.5 ± 42.5 mm), and is also the hottest month, having mean minimum and maximum temperatures of 16.3°C and 26.8°C respectively (Quin 1989). July is the coolest month (mean minimum of 6.7°C and maximum of 12.9°C), and has the lowest variation in rainfall (51.4 ± 23.1 mm).

Vegetation

The natural vegetation of Yan Yean was comprised of open forest, but previous land-use has modified the present distribution and composition of the flora. A number of prominent eucalypt associations occur in the catchment, where the term association is used to refer to dominance types: red stringybark (*Eucalyptus macrorhyncha*); red stringybark and long-leaf box (*E. macrorhyncha*–*E. goniacalyx*); red stringybark and candlebark (*E. macrorhyncha*–*E. rubida*); narrow-leaf peppermint (*E. radiata*); swamp gum (*E. ovata*); swamp gum and white sallee (*E. ovata*–*E. pauciflora*); Yarra gum (*E. yarraensis*); and river red gum (*E. camaldulensis*) (MMBW 1987). The majority of these associations form open forest on slopes and undulating lowlands, but pure stands of swamp gum and river red gum can be found on the lowest flats, forming open woodland.

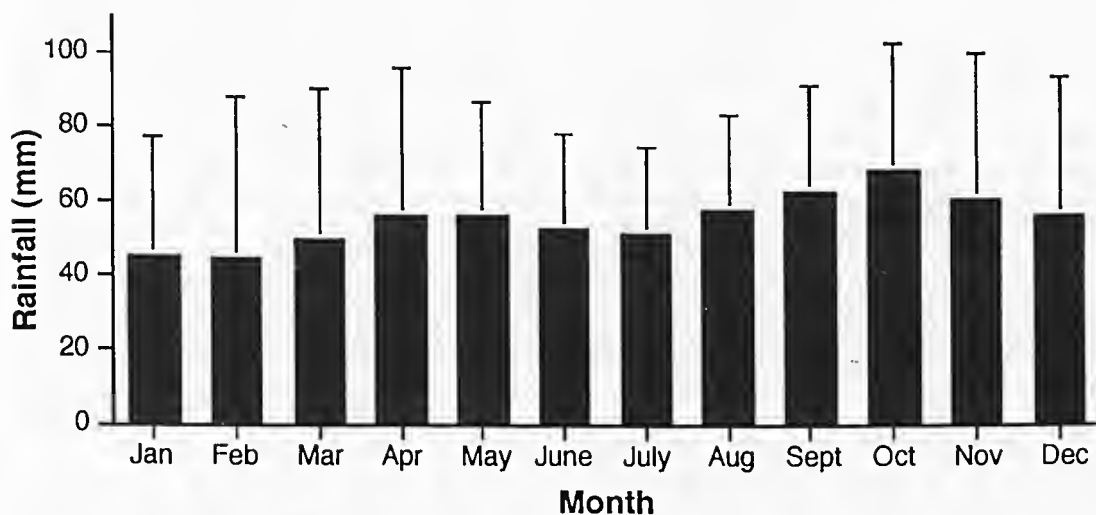


Fig. 2. Mean monthly rainfall for Yan Yean, from records taken since 1855. Error bars show standard deviations.

Of a total of 310 plant species recorded within the catchment, 43 are natives trees and shrubs. The shrub layer, when present, is dominated by wattles (*Acacia inplexa*, *A. mearnsii*, *A. melanoxylon* and *A. paradoxa*), cassinias (*Cassinia aculeata*, *C. arcuata* and *C. longifolia*) and cherry ballart (*Exocarpos cupressiformis*). The herbaceous flora is relatively rich (96 monocotyledon and 167 dicotyledon species). The ground flora is predominantly comprised of native grasses such as weeping grass (*Microlaena stipoides*), kangaroo grass (*Themeda triandra*), wallaby grass (*Danthonia* spp.), spear grass (*Stipa* spp.) and tussock grass (*Poa* spp.). The flora of the catchment also includes 66 exotic species, 19 of which are listed as serious invasive weeds in the Melbourne area (Carr et al. 1992). The invasive sweet vernal grass (*Anthoxanthum odoratum*) is particularly widespread. A number of rare and restricted species are present within the catchment, such as narrow-leaf New Holland daisy (*Vittadinia muelleri*) and clover glycine (*Glycine latrobeana*), and there are also examples of restricted remnant communities. Searlett (1983) suggested that the combined impacts of weed invasion and kangaroo grazing were having deleterious effects on the native vegetation of Yan Yean.

Habitat zones

We have distinguished five zones of kangaroo habitat at Yan Yean, each reflecting the effects of differing land use. These zones are bounded by internal tracks, catchment fences and other landmarks (Fig. 1). Three zones, East, West and South, form the major part of the catchment, which is surrounded by the 'Cyclone' security fence. The North Zone has only a standard stock fence and is separated from East Zone by an unsealed public road. The Farmland Zone lies outside the catchment proper and provides additional habitat for kangaroos. It extends westwards from West Zone to the Plenty River and northwards to the outskirts of Whittlesea. The reservoir is also exploited at times by kangaroos, providing drinking water as well as a source of food around the margins when the water level falls. Water is also available in the other zones from permanent dams constructed for fire-fighting or domestic stock, and from several perennial creeks.

North Zone. This 345-ha area has the highest point in the catchment (480 m above sea level), and has steep hills (MMBW 1987). The underlying rocks are Lower Devonian sediments of siltstone with interbedded thin sandstone (Geological Survey

of Victoria 1972). The shallow, stony gradational soils generally comprise a hydrophobic gravelly loam A horizon overlying a clayey, stony or gravelly B horizon (Jeffrey 1981; MMBW 1987). Most of the open forest in this zone is dominated by the red stringybark and long-leaf box association. The understorey varies between sparse *Cassinia* spp., *Acacia* spp. and a ground flora of *Poa* spp. on the ridges, to moderately dense undergrowth in the gullies dominated by hop goodenia (*Goodenia ovata*). This zone is relatively undisturbed both by humans and kangaroos.

East Zone. In the higher areas of this 710-ha area (up to 290 m), the underlying rocks are Lower Devonian sediments of siltstone with interbedded thin sandstone; the lower part of the zone is predominantly Silurian sandstone, interbedded with siltstone and shale (Geological Survey of Victoria 1972). The two rock types are bisected by a deposit of river alluvium consisting of sand, silt, clay and minor gravel which follows Dry Creek, an intermittent watercourse, and continues around the margin of the reservoir (Geological Survey of Victoria 1972). The soils are shallow, stony gradational soils in the higher areas, reddish duplex soils on the lower slopes, and yellow gradational soils, with an A horizon described as a clay loam, along the drainage lines (MMBW 1984). This zone consists of two designated botanical Reference Areas and their surrounding Management Zones (MMBW 1987). Yan Yean North Reference Area is representative of the remnant vegetation from low elevation open foothill forests which occur south of the Great Dividing Range, and is dominated by the red stringybark and candlebark open forest association with an understorey of *Cassinia* spp. The vegetation of Yan Yean South Reference Area is comprised of Yarra gum and red stringybark associations on the higher areas and swamp gum and white sallee on the lower areas. The understorey of Yan Yean South Reference Area is dominated by *Cassinia* spp. and *Acacia* spp. on the slopes, with austral bracken (*Pteridium esculentum*) and spiny-headed mat-rush (*Lomandra longifolia*) present in dense patches along Dry Creek. Anthropogenic disturbance of this zone has been relatively minor, as indicated by a reduced number of exotic species. Kangaroo grazing, however, may be playing a significant role in determining the species composition and structure of the understorey.

South Zone. This small (145 ha) area has the lowest relief (185–200 m). The geology consists of Silurian sandstone interbedded with siltstone

and shale, with a recent deposit of river alluvium consisting of sand, silt, clay and minor gravel at its northern edge along the reservoir margin (Geological Survey of Victoria 1972). Reddish duplex soils are replaced by yellow gradational soils with a clay-loam A horizon along the drainage lines and the reservoir margin (Jeffrey 1981; MMBW 1987). The vegetation of South Zone has been influenced by past land-use, and contains a number of naturally regenerating plantations of Monterey pine (*Pinus radiata*), blue gum (*E. globulus* ssp. *globulus*) and sugar gum (*E. cladocalyx*) that have previously been harvested. It also contains a stand of a tree-form silver banksia (*Banksia marginata*), which is unusual for this area, and a high diversity of aquatic species associated with the reservoir margin.

West Zone. The highest points in this 525-ha zone are about 250 m above sea level. The geology of this zone is dominated by Silurian sandstone, which is interbedded with siltstone and shale. A thin band of a mixture of Quaternary deposits of river alluvium consisting of sand, silt, clay and minor gravel, and similarly aged swamp deposits of silt, clay and black mud, follows an unnamed intermittent watercourse that bisects the zone (Geological Survey of Victoria 1972). The soils are similar to those of East Zone. A combination of past land-use and continued kangaroo grazing has had a significant impact on the vegetation in the West Zone. The low-lying flats and surrounding rises are mainly covered by open woodlands of swamp gum and river red gum associations, while stands of drooping sheoak (*Allocasuarina verticillata*) are found on the upper slopes. Cleared areas comprise approximately 20% of this zone and are most likely maintained by constant grazing pressure. Plantations of Monterey pine and sugar gum cover the remaining areas. Introduced species dominate the understorey: bulbil watsonia (*Watsonia meriana* cv. *bulbulifera*), blackberry (*Rubus* spp.) and sweet briar (*Rosa rubiginosa*) are common, along with grasses such as sweet vernal grass and brown-top bent (*Agrostis capillaris*). The zone also has a diverse aquatic flora along the reservoir margin.

Farmland Zone. This zone (about 400 ha) is situated mainly on the floodplain of the Plenty River and, accordingly, the geology of the low-lying areas comprises a mixture of Quaternary deposits of river alluvium consisting of sand, silt, clay and minor gravel and swamp deposits of silt, clay and black mud. These deposits are overlain by yellow gradational soils with a clay-loam

A horizon (Jeffrey 1981; MMBW 1987). The higher areas of the zone (up to 240 m) are underlain by the Silurian sandstone, interbedded with siltstone and shale, and the soils are the reddish duplex soils common to the catchment (Jeffrey 1981; MMBW 1987). The managed pasture in this zone is dominated mainly by introduced grasses such as lesser quaking grass (*Briza minor*), squirrel-tail fescue (*Vulpia bromoides*) and brown-top bent. Some native grasses persist, particularly kangaroo grass and wallaby grass, and some small stands of river red gum open woodland remain. Thickets of invasive shrubs such as hawthorn (*Crataegus monogyna*), blackberry and sweet briar are widespread.

Vertebrate fauna

A total of 37 mammal species has been recorded in the *Atlas of Victorian Wildlife* by a 5×5' grid cell centred on Yan Yean. Of these, 31 are native. Two native mammals are considered rare and are listed as threatened taxa (Schedule 2, *Flora and Fauna Guarantee Act* 1988, Victoria). These are a marsupial carnivore, the brush-tailed phascogale (*Phascogale tapoatafa*), which has been recorded in North Zone, and a riparian-dwelling bat, the large-footed myotis (*Myotis adversus*), which has been recorded in the Farmland Zone. Herbivores other than eastern grey kangaroos are uncommon: the black wallaby (*Wallabia bicolor*) and the introduced European rabbit (*Oryctolagus cuniculus*), occur at low densities in the catchment, and introduced sambar deer (*Cervus unicolor*) and feral pigs (*Sus scrofa*) are observed occasionally (Ecoplan Australia 1995).

Birds have been surveyed at Yan Yean since 1973 on an annual bird count by members of the Bird Observers Club of Australia. The count is part of the 'Challenge Count' run by the club on the first Sunday in December. The area covered at Yan Yean includes the perimeter of the reservoir, the public park below the retaining wall, and parts of South Zone, West Zone and Farmland Zone (G. Hosken, pers. comm.). A total of 155 bird species has been recorded at Yan Yean Catchment since the counts began, and only nine of these are introduced. The native species include several of conservation significance, such as the endangered regent honeyeater (*Xanthomyza phrygia*) and the rare white-bellied sea-eagle (*Haliaeetus leucogaster*). Sea-eagles have frequented Yan Yean since the 1960s, and a breeding pair nesting in a stand of sugar gum in the West Zone has been monitored closely in recent years (F. Muscolino, pers. comm.).

Yan Yean also has a rich herpetofauna. Totals of 28 species of reptiles and 18 species of amphibians have been recorded in the *Atlas of Victorian Wildlife* for the 5×5' grid cell centred on Yan Yean. All are native species, and only the glossy grass skink (*Pseudemoia rawlinsoni*) is considered to be of conservation significance, because its status is insufficiently known.

HISTORY

Indigenous people

The Wurunjerri-baluk tribes were the first human inhabitants of Yan Yean when the reservoir site was covered mostly by swamp lands (Melbourne Parks & Waterways 1995). The name Yan Yean comes from the Wurunjerri-baluk language, possibly derived from 'Yanyan', a local elder who was a signatory to a treaty that gave control of the Plenty district to white settlers; an alternative meaning is a young unmarried man, in reference to the initiation rituals that boys underwent in the area (Edwards 1978). The last of the aboriginal people left Yan Yean when there was an influx of Europeans brought in to construct the reservoir.

European settlement

Plans for the parish of Yan Yean were completed in 1838 (Jones 1992). By the 1840s, several pastoralists had either purchased land or had leased holdings in the parish (Edwards 1978). Potato and maize crops were grown throughout the 1840s and 1850s, followed by clover, lucerne, rye and other improved pasture species in the 1860s (Edwards 1978). The area was used predominantly for grazing sheep and dairy cattle, and one of the major landholders, John Bear, also cultivated orchards and vineyards covering 400 ha where the West Zone lies today (Griffiths 1992). Timber was also harvested in the catchment until the area was progressively reserved in the 1870s, and part of the East Zone served as the Upper Plenty Farmers' Common from 1874 to 1884 (Payne 1975). In 1884, 50 owners of stock were listed as grazing 402 head of cattle and 77 horses there, and it was estimated that another 100 head of cattle were using the common without a fee (Edwards 1978).

Reservoir construction

The area that is now the Yan Yean reservoir was known as Ryders Swamp by the early European settlers (Griffiths 1992). The Melbourne City surveyor James Blackburn devised the plan for a

reservoir at Yan Yean, the first reservoir constructed to supply the rapidly-growing city with water (Edwards 1978). Construction began in 1854, and the first water was supplied in a grand ceremony on 31 December 1857 (Edwards 1978). In 1872 the catchment was proclaimed a permanent reserve for water, managed by the Melbourne and Metropolitan Board of Works (MMBW), and was proclaimed a native game protection area in 1917 (MMBW 1987). From the time of its construction, Yan Yean has been a popular excursion for people from Melbourne (Edwards 1978). At its peak, from 1872–1939, it was the venue for the annual New Year's Day picnic of the 'Friendly Societies', featuring music, merry-go-rounds, highland dancing, and Punch and Judy shows. Today, Parks Victoria manages a small public park near the retaining wall in the south-eastern corner of the catchment (Melbourne Parks & Waterways 1995), which has short walks, views of the reservoir, picnic areas and barbecues, while the catchment itself is managed by Melbourne Water.

Kangaroo management

There has been a long history of complaints about kangaroos from Yan Yean's neighbours, mainly from the Farmland Zone on the western side (Melbourne Water 1982). Most complaints were about crop damage, property damage and stock feed losses. Neighbours claimed that their own destruction permits were insufficient to deal with the kangaroo problem, leading the Fisheries and Game Department to request the MMBW to cull kangaroos within the catchment. Although the MMBW was reluctant to cull on the grounds of risks to water quality and public health, the caretaker of Yan Yean was permitted to shoot a total of almost 600 kangaroos from 1954–1957. No further culling took place, although kangaroos were shot for scientific samples in the early 1960s as part of a research programme (see below). Neighbours also made repeated requests to the MMBW to erect kangaroo-proof fencing around the catchment (Melbourne Water 1982). The MMBW eventually offered to construct fencing if the cost was shared between the landholder and the board (Melbourne Water 1982), and by 1987 the entire catchment (excluding the North Zone) had been fenced with 1.8-m high chain mesh.

Kangaroo ecology

Much of the ecological research on eastern grey kangaroos in Victoria has been conducted at Yan

Yean. In 1961, the Fisheries & Wildlife Department initiated a research programme into the population ecology of the kangaroos at Yan Yean led by Keith Dempster. This work investigated age-specific fecundity and mortality, with particular emphasis on the pronounced die-off of young kangaroos (14–20 months) recorded during the winters of 1961, 1962 and 1963 (Dempster 1964). In part, this work was prompted by the potential risks to public health posed by kangaroo carcasses polluting the reservoir.

Quin (1989) subsequently analysed the population data and skulls that had been collected by the Fisheries & Wildlife Department team between 1962 and 1964. One of the major findings of his analysis were that fecundity was relatively low and seasonally dependent. Births occurred in all months of the year but reached a peak in summer, and although two-thirds of females had reached maturity by their third year, a significant proportion of mature females apparently were not breeding. The second major finding was that mortality was high, seasonally dependent and male-biased. Almost all deaths occurred during winter, and young males in their second year were heavily over-represented. Quin also found that, because the primary sex ratio was at parity, the male-biased juvenile mortality resulted in an adult population that was biased in favour of females.

Arundel et al. (1990) investigated the role of parasitic nematodes in the aetiology of the winter mortality pattern at Yan Yean in 1971 and 1972. They collected juveniles and adults over a year, and found that although adults had few nematodes at any time, juvenile kangaroos often carried heavy burdens, particularly in winter. The nematodes showing a winter peak in juveniles included *Globocephaloides trifidospicularis*, *Rugopharynx australis*, *R. rosemariae*, *Pharyngostromylus kappa*, *Macropostromylus baylisi*, *Paramacropostromylus torlaiformis* and *Strongylus* sp. Pathological

changes to the gut were evident, and there was a strong inverse relationship between numbers of *Globocephaloides trifidospicularis*, which feeds on blood, and plasma protein, haemoglobin levels, and haematocrit values. The winter peak in the life cycle of these parasitic nematodes thus coincided with the poor forage conditions and cold stresses of winter when juvenile kangaroos were most susceptible to mortality.

Brief studies were conducted in the 1970s by students of Rusden State College (now part of Deakin University). One project (Layton 1975) made some observations of the composition and activity of groups of kangaroos, and determined the age structure of a small sample of pick-up skulls. A second project (Terry 1977) made further observations of kangaroo behaviour and determined the age structure of another small sample of skulls. No further research was conducted on the population until we began our programme in 1992.

Population trends

Previous surveys of the kangaroo population at Yan Yean have been infrequent, and inconsistent in terms of the techniques used and the zones covered. The first census of the population was made in 1961, when the Fisheries & Wildlife Department conducted a drive count of East and West zones (Robertson 1985; Arundel et al. 1990). A line of people traversed half of the study area, then the other half, obtaining counts of 2200–3000 kangaroos from three separate surveys (Table 1). Although drive counts are highly accurate when conducted properly (Southwell 1989), the split procedure used in the 1961 survey may have caused errors due to under-counting if kangaroos evaded the line, and over-counting if kangaroos were counted on the first sweep then moved and were counted again on the second.

Year	Zones	Method	Population size	Source
1961	East and West	Drive count	2200–3000	Dempster (1964) Robertson (1975) -Arundel et al. (1990)
1975	East, West and South	Line transect	2935	Morgan (pers. comm.)
1992	East, West and Farmland	Line transect ^A	1770	This study
1995	North, East, West, South and Farmland	Line transect ^B	660	Morgan (1995)
1995	East, West and Farmland	Mark-resight	2109	This study

Table 1. Estimates of the size of the population of eastern grey kangaroos at Yan Yean Reservoir Catchment over four decades. ^APartial replication of Morgan's earlier transect lines. ^BSurvey conducted in two parts, two weeks apart.

No more surveys were conducted until 1975. In June, David Morgan of Melbourne State College (now part of the University of Melbourne), conducted the first survey of the Yan Yean population using rigorous line transect technique (D. Morgan, pers. comm.). He surveyed three transect lines (total length = 8.25 km), two sampling East Zone and West Zone in a roughly east-west direction, and the third sampling South Zone. Morgan stratified the area according to four habitat types (open grassland, open forest, forest/woodland with moderate understorey, forest/woodland with dense understorey). He obtained an estimate of 1.97 ha^{-1} , equivalent to almost 3000 kangaroos (Table 1).

In 1992, we carried out the next survey at Yan Yean, with the aim of replicating the survey conducted by Morgan 17 years earlier. We marked out three transect lines as close as possible to the lines used by Morgan, intending to conduct repeated surveys rather than the single survey in the 1975 study, so we could use temporal rather than spatial replication to increase precision of our estimate. We surveyed the most northerly line 12 times, and the central line 11 times. Vegetation on the third line, in South Zone, had become quite dense and visibility was poor ($<10 \text{ m}$), so this line was discontinued after three surveys. In addition, it was apparent that many kangaroos were crossing the security fence between West Zone and the Farmland Zone, so we marked out a fourth transect line (2.2 km long) in the Farmland Zone, added two other habitat types encountered in this zone (open paddock and open woodland), and surveyed the line six times. Our estimate of density (and standard error) for East and West zones together was $1.09 \pm 0.39 \text{ ha}^{-1}$, considerably lower than Morgan's estimate of 1.73 ha^{-1} for these zones in 1975. We found that density in the Farmland Zone ($1.16 \pm 0.19 \text{ ha}^{-1}$) was similar to the other zones, giving an overall estimate of 1770 kangaroos (Table 1).

The next survey was conducted in 1994 by Morgan (1995) as part of an assessment of kangaroo impacts in several reserves managed by Melbourne Water and Melbourne Parks & Waterways (Ecoplan Australia 1995). Teams of observers surveyed 14 transect lines (total length = 32.8 km), half of which ran in a roughly north-south direction, and the others ran roughly east-west. This survey systematically covered the entire catchment for the first time, including North Zone, and covered the Farmland Zone to the west. The population size was estimated to be only 660. We consider this result to be invalid, since it is far lower than both the estimate two years earlier and a second estimate using a different technique a

year later (see below). The most likely explanation for this anomalous result was that there was a two-week interval between surveys within the catchment and in the farmland, which allowed the kangaroos to redistribute themselves, thus escaping detection in one or both phases of the survey.

The following year we estimated the size of the kangaroo population using a mark-resighting method, a technique that has not often been used for kangaroos but is commonplace in studies of smaller species (Southwell 1989). We had captured and marked 58 kangaroos with individual combinations of ear tags and collars (Coulson 1996). In the course of a study of demographic variables, Penny Fannin recorded numbers of marked and unmarked kangaroos observed from a vehicle transect (length = 16 km) that sampled East, West and Farmland zones (Fannin 1995). She surveyed the transect four times, detecting a mean of 191 kangaroos, of which 2.75% were marked. Using a simple Petersen estimate (Southwell 1989), the size of the population was calculated to be 2109 kangaroos.

Overall, there is little evidence of change in the kangaroo population at Yan Yean. Despite the variety of survey techniques used and the areas surveyed, the estimates (with one exception) have ranged between 1770 and 3000 kangaroos (Table 1), and no long-term trend is evident. It might have been expected that the carrying capacity within the catchment had declined over time as exotic weeds invade and native woody species slowly regenerate on cleared areas. This prediction is supported by the lower density recorded in our 1992 replication of Morgan's survey of East Zone and West Zone in 1975. However, there are no comparable data for the Farmland Zone, so it is impossible to determine whether kangaroos could have compensated for lower carrying capacity in the catchment by making greater use of neighbouring farms. There is an obvious need for a survey regime that is comprehensive, systematic and repeatable, so that population trends can be monitored in the future. We have now established a set of 15 permanent, east-west transect lines (total length = 33.1 km) in the East, West, South and Farmland zones, giving a higher sampling intensity than any previous survey. The lines have been surveyed annually, beginning in the summer of 1996-97.

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REFERENCES

- ARUNDEL, J. H., DEMPSTER, J. K., HARRIGAN, K. E. & BLACK, R., 1990. Epidemiological observations on the helminth parasites of *Macropus giganteus* Shaw in Victoria. *Australian Wildlife Research* 17: 39–51.
- BELL, H. M., 1973. The ecology of three macropod marsupial species in an area of open forest and savannah woodland in North Queensland, Australia. *Mammalia* 37: 527–544.
- CARR, G. W., YUGOVIC, J. V. & ROBINSON, K. E., 1992. *Environmental Weed Invasions in Victoria: Conservation and Management Implications*. Department of Conservation & Environment and Ecological Horticulture Pty Ltd, Melbourne, 78 pp.
- CAUGHLEY, G., 1964. Density and dispersion of two species of kangaroo in relation to habitat. *Australian Journal of Zoology* 12: 238–249.
- COULSON, G., 1996. A safe and selective draw-string trap to capture kangaroos moving under fences. *Wildlife Research* 23: 621–627.
- COULSON, G. M. & RAINES, J. A., 1985. Methods for small-scale surveys of grey kangaroo populations. *Australian Wildlife Research* 12: 119–125.
- DEMPSTER, J. K., 1961. Kangaroo management in Victorian agricultural areas. *Journal of Agriculture* 59: 45–52.
- DEMPSTER, J. K., 1964. Control and conservation of kangaroos in Victoria. In *Australian Vermin Control Conference 1964*. CSIRO, Melbourne, E 1–2 (unpublished).
- ECOPLAN AUSTRALIA PTY LTD, 1995. *Macropod and rabbit study report: Yan Yean Catchment and Reservoir Park, Plenty Gorge Park, Cardinia Catchment and Reservoir Park and Sugarloaf Catchment and Reservoir Park*. Report for Melbourne Water and Melbourne Parks & Waterways, Melbourne, 97 pp. (unpublished).
- EDWARDS, D., 1978. *Yan Yean: a History*. Yan Yean School Council, Yan Yean, Victoria, 109 pp.
- FANNIN, P. J., 1995. Observed rate of increase and demography of the Eastern Grey Kangaroo, *Macropus giganteus*. BSc(Hons) Thesis, Department of Zoology, University of Melbourne (unpublished).
- GEOLOGICAL SURVEY OF VICTORIA, 1972. Yan Yean Map-sheet. Pt 7922. Zone 55. Australia, 1:63 360.
- GRIFFITHS, T., 1992. *Secrets of the Forest. Discovering History in Melbourne's Ash Range*. Allen & Unwin, St Leonards, New South Wales, 212 pp.
- HILL, G. J. E., 1981. A study of habitat preferences in the grey kangaroo. *Australian Wildlife Research* 8: 245–254.
- HILL, G. J. E., BARNES, A. & WILSON, G. R., 1988. The use of wheat crops by grey kangaroos, *Macropus giganteus*, in southern Queensland. *Australian Wildlife Research* 15: 111–117.
- JEFFERY, P. J., 1981. *A Study of the Land in the Catchments to the North of Melbourne*. Soil Conservation Authority, Melbourne, 70 pp.
- JONES, M., 1992. *Nature's Plenty: History of the City of Whittlesea*. Allen & Unwin, St Leonards, New South Wales, 319 pp.
- LAVERY, H. J. & KIRKPATRICK, T. H., 1985. Kangaroos as pests. In *The Kangaroo Keepers*, H. J. Lavery, ed., University of Queensland Press, St Lucia, Queensland, 103–132.
- LAYTON, P., 1975. An ecological study of the grey kangaroo (*Macropus giganteus*) at Yan Yean Reservoir, Victoria. Department of Environmental Studies, Rusden State College, Clayton, Victoria, 16 pp. (unpublished).
- MELBOURNE PARKS & WATERWAYS, 1995. *Yan Yean Reservoir Park Setting Plan*. Planning Services and Planning & Environment Division, Melbourne Parks & Waterways, Melbourne, 26 pp. (unpublished).
- MELBOURNE WATER, 1982. *Kangaroo problem: Yan Yean*. Resume of File 57/9654. Operations Division, Watersheds Department, Melbourne Water, Melbourne, 7 pp. (unpublished).
- MMBW, 1987. *Yan Yean Reference Areas Management Plan*. Forestry & Land Management Section, Melbourne & Metropolitan Board of Works, Melbourne, 36 pp. (unpublished).
- MMBW, 1989. *Water for Melbourne*. Melbourne & Metropolitan Board of Works, Melbourne (brochure).
- MORGAN, D., 1995. *Macropod Populations in the Four Melbourne Parks and Waterways reserves, 1994*. Report to Ecoplan Australia. The University of Melbourne Zoology Department, Melbourne, 89 pp. (unpublished).

- NEAVE, H. M. & TANTON, M. T., 1989. The effects of grazing by kangaroos and rabbits on the vegetation and the habitat of other fauna in the Tidbinbilla Nature Reserve, Australian Capital Territory. *Australian Wildlife Research* 16: 337-351.
- PAYNE, J. W., 1975. *The Plenty: A Centenary History of the Whittlesea Shire*. Lowden Publishing, Kilmore, Victoria, 234 pp.
- POOLE, W. E., 1982. *Macropus giganteus*. *Mammalian Species* No. 187: 1-8.
- QUIN, D. G., 1989. Age structures, reproduction and mortality of the Eastern Grey Kangaroo (*Macropus giganteus* Shaw) from Yan Yean, Victoria. In *Kangaroos, Wallabies and Rat-kangaroos*, G. Grigg, P. Jarman & I. Hume, eds, Surrey Beatty & Sons, Chipping Norton, New South Wales, 787-794.
- ROBERTSON, D., 1985. Interrelationships between kangaroos, fire and vegetation dynamics at Gellibrand Hill Park, Victoria. PhD Thesis, University of Melbourne, Australia (unpublished).
- SCARLETT, N., 1983. *Floristic Survey of Grassy Open Forests in the Yan Yean Catchment Area*. Report to Melbourne & Metropolitan Board of Works. La Trobe University, Botany Department, Bundoora, Victoria, 11 pp. (unpublished).
- SOUTHWELL, C., 1987. Macropod studies at Wallaby Creek II. Density and distribution of macropod species in relation to environmental variables. *Australian Wildlife Research* 14: 15-33.
- SOUTHWELL, C., 1989. Techniques for monitoring the abundance of kangaroo and wallaby populations. In *Kangaroos, Wallabies and Rat-kangaroos*, G. Grigg, P. Jarnan & I. Hume, eds, Surrey Beatty & Sons, Chipping Norton, New South Wales, 660-693.
- TAYLOR, R. J., 1984. Foraging in the eastern grey kangaroo and the wallaroo. *Journal of Animal Ecology* 53: 65-74.
- TAYLOR, R. J., 1985a. Habitat use by the eastern grey kangaroo and wallaroo in an area of sympatry. *Mammalia* 49: 173-186.
- TAYLOR, R. J., 1985b. Effects of pasture improvement on the nutrition of eastern grey kangaroos and wallaroos. *Journal of Applied Ecology* 22: 717-725.
- TERRY, L., 1977. Studies of the eastern grey kangaroo (*Macropus giganteus*) at Yan Yean Reservoir. Department of Environmental Studies, Rusden State College, Clayton, Victoria, 19 pp. (unpublished).

TRANSACTIONS
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ROYAL SOCIETY OF VICTORIA
1998 J. E. CUMMINS ORATION

Delivered by CAMPBELL McC. ANDERSON
Managing Director, North Limited

CAUTION: PRECAUTIONARY PRINCIPLE AT WORK

President and Members of the Royal Society,
Guests,

As the 25th J. E. Cummins Memorial Orator, I am honoured to join the distinguished company of speakers who have preceded me and, even more so, to realise that I am one of the few business people to have been invited to deliver this annual address. The Society is to be congratulated on continuing the work of Jack Cummins in seeking to build bridges between industry and science.

In one sense, this is a task that looks unnecessary. Industry and science have always been closely linked. Modern industry would not exist without science—and this is especially true of the resource industries in which I have made my life. Yet, in more recent times industry and science have not exactly been the complementary institutions they would seem to be.

In today's disputatious world, science and industry often find themselves on opposite sides of arguments. Perhaps I should refine that thought a little. It seems to me that, in the conflicts that do arise between science and industry, the antagonists are most commonly the economic rationalist side of industry and the research arms of science. One accuses the other of too great a regard for money, and the comeback is that the people in the white coats should take a reality check.

My concern here tonight is not to argue the business case, nor to decry the sincerely held and soundly based opinions of scientists. Indeed, I would say that business and science should not be in constant agreement. My first economics professor once told me that if two people agreed then one of them wasn't thinking. Although not entirely agreeing with this statement I have no doubt that there should be an interchange of constructive criticism. Intelligent debate is good for all of us.

What I want to do, however, is suggest an alternative basis for that debate—and I have chosen the so-called 'precautionary principle' as my subject because it is a frequent flashpoint today for conflict between business and science. It is supported by many reputable scientists. It is denied by many reputable business people. It is a principle which

calls science into question, and it is a principle which asks business to alter one of its own fundamentals, the approach to managing risk.

DEFINITION AND HISTORY

The precautionary principle is most often invoked in the development and implementation of environmental protection policy. It has become a fundamental of international environmental law and it seems now to be extending into other areas of politics and social policy. The precautionary principle is proving to be one of the most powerful political ideas of our age.

It is also one of the most elusive. There are as many commonly accepted explanations as there are political advocates. There is no single definition. Even in international treaties and declarations the precautionary principle has at least 12 different definitions and these definitions themselves are subject to widely varying interpretations.

The precautionary principle emerged from a German concept which sought to absorb the multiple notions of risk prevention, cost effectiveness, ethical responsibility towards maintaining the integrity of natural systems and the fallibility of human understanding. A loose and open-ended interpretation of precaution can be used to justify not only general planning in the economy, but also in technology, in morality and in social initiatives.

In 1976, the then West German Government made a first attempt at encapsulating these ideas in environmental law. It stated, in retrospect rather mildly: 'Environmental policy is not fully accomplished by warding off imminent hazards and the elimination of damage which has occurred. Precautionary environmental policy requires furthermore that natural resources are protected and demands on them are made with care.'

The precautionary principle went international through the 1987 Ministerial Declaration of the Second Conference on the Protection of the North

Sea. The focus on this declaration was on 'reducing polluting emissions of substances that are persistent, toxic and liable to bioaccumulate at source, by the use of the best available technology and other appropriate measures. This applies especially when there is reason to assume that certain damage or harmful effects on the living resources of the sea are likely to be caused by such substances, even where there is no scientific evidence to prove a causal link between emissions and effects (the principle of precautionary action)'.

The principle was quickly adopted into numerous multilateral treaties and international declarations, including the 1987 Montreal Protocol on Substances that Deplete the Ozone Layer, the 1992 Convention on Biological Diversity, the 1992 Climate Change Convention, the 1992 Treaty on European Union, the 1992 Convention for the Protection of the Marine Environment of the North-East Atlantic and the 1992 Helsinki Convention, dealing with protection of the marine environment of the Baltic.

Parties to the London Convention of 1972, governing the control of ocean dumping, embraced the precautionary approach in 1991. International declarations containing the precautionary principle include the 1990 Bergen Declaration on sustainable development and the 1992 Rio Declaration on Environment and Development.

At the Rio Earth Summit in 1992 the Precautionary Principle was Principle 15 of 27 principles that made up the Rio Declaration on Environment and Development. That definition of the Principle states —'where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation'.

In Australia, the precautionary principle now underpins much of our own environmental law and policy. The Inter-Governmental Agreement on the Environment (IGAE) defines the principle thus:

'Where there are threats of serious or irreversible environmental damage, lack of full scientific certainty should not be used as a reason for postponing measures to prevent environmental degradation. In the application of the precautionary principle, public and private decisions should be guided by:

- (i) careful evaluation to avoid, wherever practicable, serious or irreversible damage to the environment; and*
- (ii) an assessment of risk-weighted consequences of various options.'*

While this IGAE definition refers to practicability, it makes no reference to 'cost effective

measures' as does the Rio Declaration principle and therefore, although appearing to be reasonable, is still open to conflicting interpretations in its application. Nevertheless, it focuses on the important issues:

- the unacceptability of serious or irreversible environmental damage; and
- where necessary the need to take preventative measures based on careful evaluation and risk assessment of the options.

I would particularly draw your attention to the two provisos given. The Australian definition clearly provides that, in the application of the precautionary principle, decisions should be guided by careful evaluation and an assessment of the risks of different options. These two fundamental tenets of evaluation and risk assessment are too often left off in reference to, and the application of, the principle and it is these omissions that I suggest lead to its misuse.

The Minerals Council of Australia (MCA), after thoroughly researching and debating the principle, embraced it and advocate its application through comprehensive evaluation and risk assessment processes. The Code of Environmental Management of the Australian Minerals Industry is the blueprint for putting these processes into operation, although the Code makes no direct reference to the precautionary principle. The MCA believes that the greatest value of such a precautionary approach is achieved when it is applied in a manner that is compatible with the other Rio Declaration Principles that promote both equitable development and environmental protections.

The MCA also recognises that the valid application of its precautionary approach needs to be tested and has therefore adopted a review and reporting system.

APPLICATION OF THE PRINCIPLE

As a member of the Council, I agreed with the MCA's position and therefore can be said to be supportive of the precautionary principle, but only when it is appropriately conditioned by the provisos of evaluation and risk assessment. For the purposes of this address I will refer to this as the 'risk assessed precautionary principle'.

My concern, however, is that the precautionary principle to which reference is often made is not so conditioned and is founded on a simple idea that most people would regard as common sense—that is, if there is an identified risk of something going seriously wrong with an action, then don't do it.

The application of such common sense, however, does not provide us with even a basic understanding of the complex evaluation processes and risk assessments that are now undertaken in addressing the environmental, economic and social aspects of our actions. Common sense tells us that burning coal increases the greenhouse effect and should stop. Common sense demands that dangerous uranium be left in the ground. Where such common sense might leave our common human need for energy in an increasingly common high-tech age is, however, not commonly addressed. Common sense is often misleading, and in its apparent support for the precautionary principle, I suggest that it is wrong.

The precautionary principle, taken to extremes, is a recipe for doing nothing. If we as human beings accepted no risk in our lives, we would not eat nor drink nor breathe. The precautionary principle, in its simplest form, would kill us.

Of course, none of the vast array of definitions and interpretations of the precautionary principle even suggests such extreme consequences. The written laws and policies based on the principle are couched in terms of sweet reason. At their best, they seek a balance between action and caution. But the application of the principle invites extremes that can and often do result in irrational decisions and the erosion of scientific method and integrity.

Application of the precautionary principle has led to demands that the proponent of an action, whether it be the developer of a new mining project or the marketer of a new pharmaceutical, prove that a feared result will *not* occur. This is meant to devolve to an assessment of risk and carefully thought-through decisions based on probabilities. If only it did. More and more, through reference to the precautionary principle, governments are being pressured not to behave on such rational grounds.

The notion that any activity should not commence until it is proven in absolute terms that there is no risk in that activity is an absurdity based on either a lack of understanding of risk or an irrational approach to managing it.

What many environmental activists have sought to do is to turn the precautionary principle's quite legitimate requirement for caution in the face of scientific uncertainty into a totally illegitimate demand for absolute scientific certainty that proposed actions carry no risk. This neat little semantic distortion then, as often as not, leads to the rejection of scientific assessments with which they do not agree. For the purposes of this address I will refer to this interpretation as the unconditional (or negative) precautionary principle.

To quote Greenpeace: 'A precautionary approach to environmental protection requires the use of clean production techniques, innovative solutions and social and consumer change to achieve an ultimate goal of zero discharges of harmful substances to the environment.' An admirable goal, you might say, but think about it: what is the definition of 'harmful'? The natural expiration of all air-breathing animals contains carbon dioxide—the gas identified as the main culprit in global warming. Similarly, all industries emit substances to the environment. All those substances could be demonstrated to be harmful in some way, depending upon how 'harmful' is defined.

Again, this is extremist, and Greenpeace would undoubtedly deny that it mean to go that far. On the other hand, Greenpeace does not readily accept scientific assessment of risk, and decisions based on such scientific assessment, I quote again: 'The technique of risk assessment is supposed to weigh up scientifically the risks of a given act so that a decision can be made about whether it is acceptable. In reality, the process of risk assessment inevitably involves many value judgements and assumptions. Is it really a sound basis for environmental decisions?'

This question provides the core of my address and without hesitation, my answer to this question is 'yes'.

SCIENCE AND RISK

Writing in *The Australian Geologist* magazine in March this year, Cliff Ollier of the University of the South Pacific observed: 'Scientists can only make reasoned judgements based on current knowledge and ideas. In contrast, use of the precautionary principle abandons not only scientific proof, but the concept of proof itself. The precautionary principle is not so much anti-science as anti-reason. It legitimises unfounded fears and raises irrational decision-making to an art form.'

What then is the alternative to the precautionary principle? The British Government, a confirmed advocate of the principle, says environmental policy must be based on what it calls 'sound science'.

But what is 'science' exactly, and what constitutes 'sound science'? There will be no consensus in answers to either of these questions but examination of them should clarify our thinking on science's role in assessing risk.

Science has two common public faces—that of successful technology, and that of pure research. Neither of these is much help in our dilemma. We should use our own precautionary principle in adopting either or both as a description of science.

A third facet of what might constitute science is that it is a body of knowledge that is proved beyond doubt. Given the impossibility of being absolutely sure about anything, this third aspect in reality should only be an item on some politician's wish list.

There is, however, one definition of science and its corollary, sound science, that attracts me and it was given recently in the journal *Science and Public Affairs*, published by the Royal Society and the British Association for the Advancement of Science in which Dr David Fisk, Chief Scientist of the British Department of the Environment, put it this way:

'Science is defined as a state of knowledge about the real world which includes both interpretations of data that are held without dispute and interpretations that are viewed as speculative. Science is quality-assured as sound by the process through which it is assembled.'

This definition of science does not deny the uncertainty of science, but neither does it minimise its importance. Rather, it gives us a basis from which we can move to the assessment of risk, a concept which is of course itself fraught with definitional difficulties.

'Risk' is a four-letter word that has already featured strongly in this address. It is an idea that might be said to be understood by all—something like science in that respect. But is it really understood and in particular is it understood in the context of business and rational decision-making?

I have recently been reading a book called 'Against the Gods—the Remarkable Story of Risk' by Peter L. Bernstein, a funds manager with one of the major New York institutions. The book is now a couple of years old but it deals in timeless concepts. I have been fascinated by the evolution of these concepts from notions of how to win at gambling to current sophisticated management techniques.

Bernstein notes that in the early 18th Century Abraham de Moivre, the inventor of what is commonly known as the Law of Averages, defined risk as the chance of a loss. 'The risk of losing any sum,' de Moivre said, 'is the reverse of expectation and the true measure of it is the product of the sum ventured multiplied by the probability of the loss.' Since then, some of the world's best minds have provided us with complex tools with which to manage risk.

Risk management in this context is, of course, about economics. It is about money and profits and standards of living—all those things that are

fundamental to business, but are anathema to the stated environmental philosophy that environmental protection and conservation must always have a higher priority than economics. How can you, they ask, put a dollar value on an environmental asset?

But economics is about people and their needs; it is not just disembodied numbers on a page. There will therefore be times when difficult choices have to be made between economic gain and irreversible adverse environmental change. In developing countries, for example, governments seeking quite modest but necessary increases in the living standards for their people have deliberately made trade-offs against environmental changes which in countries like Australia would not be countenanced.

How can we—well fed, well clothed, and comfortable—say this is not justified? Surely we should not deny other people the material benefits of industry that we have obtained. Let us not forget that at some time in the past, we too have made the trade-off between wilderness and development, although not as consciously as is so often today demanded of other people.

I personally do not believe we have that right, but many environmental activists do insist that the peoples of developing countries should not take the risks we have—that because of the uncertainty, they should do nothing. I believe that, while we in the developed world have choices that are much less stark, no people should be asked to sacrifice their future on the altar of uncertainty.

John Maynard Keynes recognised that 'as living and moving beings, we are forced to act ... [even when] our existing knowledge does not provide a sufficient basis for a calculated mathematical expectation'. In other words, human nature is such that we will always be obliged and indeed willing to take risks.

Another eminent economist of a slightly earlier vintage, Frank Knight, treated risk and uncertainty as separate concepts, not as synonyms. He saw risk as being a measurable uncertainty. He observed: 'It will appear that a measurable uncertainty, or risk proper ... is so far different from an unmeasurable one that it is not in effect an uncertainty at all.' My conclusion from reading Knight is that if we assess uncertainties properly most, if not all, risk can be diminished to manageable, or even vanishing, proportions. We should not be afraid of uncertainty.

This is the essence of risk assessment—the systematic identification, analysis and evaluation of uncertainties in an enterprise, so that they can be measured and therefore manageable. And this is where business again must depend on science.

In physical environments, business must call on science to provide the measurements so that risk can be assessed and thereafter managed.

Pereceptions of this relationship between business and science do, however, vary greatly. Some sections of business would see science as being required to guarantee the correctness of its environmental risk assessment, thereby providing the absolute assurances of safety that everyone should realise are impossible. Some sections of science, for their part, would be equally busy denying that their work should be, or even could be, the basis of assessments used to make environmental risk manageable. Neither position adds anything to the debate and only serves to strengthen the precautionary principle, which, as Greenpeace notes is increasingly becoming the link between science and policy.

Britain's Chief Scientist, David Fisk, in his article to which I referred earlier, points out that scientific method allows for no time limits and no final decisions, opposites to management imperatives. 'To take the short cut to decisions,' he writes, '... other disciplines add in various risk management philosophies. It does not help our thinking if we include the process of risk analysis in a definition of a sound science process.'

Fisk says risk assessments, while based on sound science, should be treated as a distinct process that follows the scientific assessment. At the same time, wearing his policy-maker's hat, he warns his fellow scientists that risk assessments can and should never be done outside a policy framework; in other words, scientific data alone will never decide the level of risk attached to any proposed action.

SCIENCE AND BUSINESS

Scientists should not, however, interpret the above as a call for them to abdicate responsibility for the use of their data. I said at the outset that I believe we all gain from constructive criticism and intelligent debate. Scientists should be willing and able to offer a point of view along with their data. What they should *not* do, however, is allow their opinions to affect their data and thereby to interfere with 'sound science'.

Yet this is what the precautionary principle encourages, and I fear some scientists have gone along with it, albeit with the best intentions. They are misguided to believe they can head off undesirable outcomes from industrial development by agreeing with Greenpeace and its ilk that scientific uncertainty translates directly to unacceptable risk.

Equally, we in business need to acknowledge that some risks are indeed unacceptable. Our critics will demand examples but this is simply rhetoric. Those risks that business finds unacceptable are embodied in projects that never see the light of day. Development projects that reach the proposal stage can be assumed to have embedded in them the business belief that any environmental risk can be managed effectively.

Exposure and public discussion is then necessary to challenge such business belief—it thereby allows the issues attached to the relevant risk to be teased out and subjected to rigorous scrutiny by relevant authorities within what are frequently onerous policy frameworks. Business, legitimately, argues its case vigorously, as its opponents argue theirs.

Science should be reassured. The system, when it is allowed to do so, does work. Those scientists with such deeply and sincerely held beliefs about environmental care that they can admit to no other priority will not be consoled but others on the borderline should find a positive message that debate with business is not futile. They should not feel they have to use the highly dubious and negative precautionary principle to have their views properly considered.

The absence of a common understanding and approach to scientific evaluation and risk assessment in decision making has often led to misunderstanding and even distrust between business and scientists. It is, however, pleasing to note that there have recently been increasing efforts for joint analysis of this issue in attempts to develop better assessment mechanisms. These attempts need to be successful if the distrust is not to grow.

CONCLUSION

My purpose in this address has been to examine the precautionary principle with a view to suggesting a different emphasis to the debate between business and science, and thereby furthering the cause of building or maintaining bridges between the two.

The principle has many definitions and interpretations around the world but in Australia it is generally stated along the lines that, where there are threats of serious or irreversible environmental damage, lack of full scientific certainty should not be used as a reason for postponing measures to prevent environmental degradation. But neither should it be used as an automatic prohibition to development. Rather it must be the basis for the assessment of risk.

The precautionary principle has become one of the more powerful political ideas of our time but if it is applied in an unconditional manner, it does not stand up to logical analysis and can be inherently subjective—the potential consequences of which are economic stagnation and scientific corruption.

In its unconditional form it is a major flashpoint for conflict between industry and science because:

- (a) it demands of industry proof that an action will *not* cause environmental harm and it is impossible for science to deliver an absolute assurance to that effect; and
- (b) it admits of no risk in human enterprise (and unfortunately many scientists in pursuit of environmental protection are attracted to this notion as a defence against what they see as depredations of development).

The precautionary principle equates uncertainty with risk but I suggest that more often than not risk is really a measurable uncertainty and, if treated properly, can be reduced to manageable proportions. Environmental risk must be seen as being susceptible to scientific identification, analysis and assessment, from which decisions

about development can be taken within an established policy framework.

I recognise that the precautionary principle is not about to disappear, but it needs to be more rigorously assessed in line with the stated principles of evaluation and risk assessment. Misuse of an unconditional precautionary principle will erode its credibility. Business must live with the principle, but the way to achieve satisfactory outcomes is through risk assessment based on sound scientific input. Business therefore needs scientific honesty—data and opinions untainted by over zealous application of the unconditional precautionary principle. In return scientists are entitled to expect that business will rigorously review and apply the latest knowledge and also accelerate the development of better performance measures.

By all means let the environmental debate between business and science roar ahead. I emphasise once again that it is healthy and desirable, no matter how uncomfortable it might make the business world.

Let the debate be based, however, on proper assessment of risk, so that business can continue its historic role of building economies and creating wealth without an overdose of caution.

Let us not sacrifice the future on the altar of uncertainty.

ECOLOGICAL SUSTAINABILITY IN THE VICTORIAN ALPS

Royal Society of Victoria Symposium, Melbourne, 15 November 1997

INTRODUCTION

A scientific symposium was held by the Royal Society in the Laby Theatre, The University of Melbourne on 15 November 1997. The topic was 'Ecological Sustainability in the Victorian Alps'. A range of speakers from diverse backgrounds including geology, biology, ecology, agriculture, government and the university sectors provided a spectra of presentations and viewpoints.

A few of the speakers have provided short summaries of their presentations which are included in these *Transactions* in order to stimulate further research, debate and the exchange of information and opinion concerning one of the major ecological areas within Victoria.

THE IMPACT OF LAND COVER CHANGES ON HYDROLOGICAL SUSTAINABILITY IN THE VICTORIA ALPINE AREA

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The alpine region of Australia is important for its water resources and yet land usage in the past has not always been conducive to hydrological sustainability. In this paper, hydrological data from eight streams in the Bogong High Plains area are analysed for the impacts of three different land cover changes on streamflow. The 1939 bushfire was noticed to affect storm runoff and daily streamflow immediately after the event, but those changes were not statistically significant. An insect plague in the grasslands north of Mt Cope produced an increase in runoff in Cope Creek for the following five years. Mining for gold at the Red Robin Mine north of Mt Hotham has occurred almost continuously since 1940. The period of intensive mining operations in the mid 1960s produced lower monthly runoff than occurred either before or after that time. Land use practices to encourage hydrological sustainability in alpine areas is discussed.

AT A national level, the snow country of south-eastern Australia is one of the most efficient water producing areas in the country. Along with other areas in the northern and eastern margins of the continent and in Tasmania, the Australian alpine area receives a median annual rainfall in excess of 1200 mm and contributes an average annual runoff greater than 500 mm (Brown 1983). However, unlike the other high runoff areas mentioned, the Australian alpine area has a very low level of hydrological variability. This is significant because Australia has the most variable rainfall and streamflow in the world (McMahon et al. 1992).

The importance of the Australian Alps for national water yield is illustrated by an examination of the rivers emanating from the Alps. The Murray-Darling River system is the largest catchment in the country covering more than 1 000 000 km² and contributing 1440 mm mean annual runoff (Crabb 1997). Of the 26 major catchments within the Murray-Darling system, there are four catchments that drain most of the Australian Alps—the Upper Murray, Kiewa, Ovens and Goulburn rivers. Although these four catchments only occupy 4% of the Murray-Darling system, they contribute 70% of the annual runoff. The catchment that produces the most water is the Kiewa River, which has a mean annual runoff of 344 mm (average value is 55 mm). Rowe (1972) calculated that 23% of the total yield of the Kiewa River comes from the 8% of land located above 1500 metres.

Given that the Australian alpine area produces so much runoff in a country where water resources

are scarce (Commonwealth of Australia 1996), it is important that catchment management practices are conducive to both ecological and hydrological sustainability. However, the history of land usage in the Australian alpine area has generally resulted in land and water degradation rather than sustainability (Kirkpatrick 1994; Lawrence 1994; Wahren et al. 1994). Controversy over appropriate land management practices has been a feature of the history of the Australian Alps and continues to the present day. This paper details some land use practices which have altered the land cover and hydrological characteristics of one section of the Australian alpine area—the Bogong High Plains in northeastern Victoria.

THE BOGONG HIGH PLAINS

In northeastern Victoria, the mountain ranges which comprise the Australian Alps are composed of a series of elevated plateaux separated by steep-sided and incised valley systems. The Bogong High Plains are the largest of these plateaux areas, and together with the summits of Mt Bogong, Mt Hotham and Mt Feathertop carry Victoria's ten most elevated peaks. Rivers draining from the Bogong High Plains include the Kiewa River, Ovens River, Dargo River, and tributaries of the Mitta Mitta River. The fact that the Kiewa River contributes the highest average annual runoff per unit area of all the Murray-Darling River catchments is largely due to the presence of the Bogong High Plains in the catchment headwaters.

The distinctive nature of the Bogong High Plains area owes its character to a unique combination of climatic, geological, geomorphological and vegetation characteristics. The plateau area is located above 1500 m elevation, and typically receives more than 2000 mm precipitation per annum, much in the form of snow for several months each year. Geologically, most of the area is underlain by metamorphic rocks such as granodiorite, gneiss and schist, and the Mt Feathertop area is composed of steeply dipping slates. The Bogong High Plains are regarded as a palaeo terrain that has been uplifted but has maintained its character because the plateau areas have remained unaffected by headward erosion (Beavis 1962). The great diversity of landscape components has given rise to a large variety of vegetation types. The lower altitude areas carry mixed species forests dominated by stringybarks and peppermints, which give way to alpine ash forests (*Eucalyptus delegatensis*) between about 800 and 1400 m elevation, and snow gum woodlands (*E. pauciflora*) above that. The vegetation of the plateau areas is typified by a mosaic of snow gum woodlands, heathlands, grasslands and mosslands (McDougall 1982), and the truly alpine areas are restricted to three or four of the highest peaks.

The diversity of geomorphological and vegetation characteristics of the area has resulted in extensive land use activity over the last few thousand years. The Aborigines of northeastern Victoria utilised the aestivating Bogong moth (*Agrotis infusa*) for many centuries prior to European settlement but their impacts on the environment were minimal (Flood 1980). Since the first European discovery of the area in 1851, the natural resources of the area to be utilised have included the alpine grasslands for summer grazing, the mineral wealth for economic gain, the water resources for hydroelectric development, the forest resources for timber, the open area and snow fields for recreation, and the unique mountain environment for nature conservation (Lawrence 1994). Today, the Bogong High Plains and surrounding valleys are mostly contained within the Victorian Alpine National Park (Slattery 1998).

Associated with the multiple land usage of the Bogong High Plains have been both severe and subtle land cover changes. Most concern has been directed to the role of introduced stock on the subalpine ecology (Australian Academy of Science 1957; Costin 1957; Williams & Ashton 1987; McDougall 1989; Wahren et al. 1994) and catchment value of the area (Costin et al. 1959; Lawrence 1995). The role of other land cover changes has also received some attention. Costin (1957) outlined the impacts of grazing, fire and

construction activities on the Bogong High Plains in the mid 1950s. Fluin (1995) examined the impact of ski village sewage disposal on the water quality of receiving streams, and Lawrence (1994) proposed a time series model to link vegetation changes on the Bogong High Plains with both extensive and intensive land uses. This paper examines the impacts of both the 1939 bushfire on several subalpine and mountain streams on and north of the Bogong High Plains, insect attack on the grasslands near Mt Cope, and gold mining operations associated with the Red Robin Mine on the hydrology of the West Kiewa River draining from the Mounts Hotham and Feathertop areas.

Elsewhere in mountain and subalpine Australia, there have been several studies examining the impacts of bushfire on hydrological characteristics. Many authors have documented that immediately following bushfire, increases in streamflow were observed (McArthur 1964; Brown 1972; Mackay et al. 1980; Kulik 1990). McArthur (1964: 115) cited evidence of greatly increased streamflow from the Victorian Alps following bushfire and claimed the following:

High intensity fire produces an immediate and spectacular increase in streamflow. During the extremely severe fire period of January, 1939, in Victoria, one catchment of 26.5 square miles [68.6 km²] in the Bogong High Plains was burnt and an adjoining catchment of 28.5 square miles [73.8 km²] remained unburnt. Both catchments carried comparable sub-alpine vegetation ...

In the absence of rain, relative streamflow increased by seven cusecs [0.2 m³/s] after the fire and is equivalent to 3.8 million acre feet [4700 million m³] per day. This represents a water loss of 0.01 inches [0.25 mm] per day and probably reflects the transpiration losses from shrubs and lower canopy levels. The relative increase of 16 cusecs [0.5 m³/s] after the rain period reflects the greatly increased runoff from a severely burnt forest.

In *E. regnans* forest in north-central Victoria, Langford (1976), Kuczera (1987) and Jayasuriya et al. (1993) reported that following the initial increase in streamflow after the 1939 bushfire, there was a significant reduction in streamflow for several years after the fires depending on the type of vegetation found in the burnt catchments. Many of these studies considered catchments containing subalpine vegetation communities and each demonstrated a substantial alteration to pre-fire flows.

There is no known study examining the hydrological response of insects defoliating vegetation stands in Australia, although Love (1955) and Bethlahmy (1974) reported that a beetle infestation

in a spruce forest in Colorado resulted in an average annual increase in streamflow up to fifteen years after the outbreak.

Two authors have reported on the effects of mining on runoff properties in Australia. Loh et al. (1984) reported an annual increase of 48 mm runoff sustained for the eleven years that a bauxite mine was operating in southwestern Australia. Likewise, Ruprecht (1991) documented streamflow increases of 8 to 20% of annual rainfall in an adjacent bauxite mine area. In the later study, the proportion of streamflow increase was related to the area of catchment mined. Although neither of these studies focused on the subalpine area, it is expected that the runoff from the Bogong High Plains area would respond similarly if subjected to mining activities.

HYDROLOGICAL DATA AND ANALYSES

To identify possible changes to the hydrology of areas subjected to bushfire, insect attack and mining activities, streamflow data collected by the Victorian State Electricity Commission for the

construction and operation of the Kiewa Hydro-Electric Scheme was acquired. This data was subjected to, and satisfied, rigorous quality testing (Lawrence 1990). Daily and monthly hydrological data were utilised for the period of record for the eight catchments detailed in Table 1. The catchments of the East Kiewa and West Kiewa Rivers are juxtaposed to each other and the catchments of the Rocky Valley and Pretty Valley Streams together constitute the East Kiewa River drainage system. The Rocky Creek and Rocky Valley Creek catchments are nested within the Rocky Valley Stream catchment, and the Cope Creek and Pretty Valley Creek are tributaries of the Pretty Valley Stream (Fig. 1).

It was desired to take a paired catchment approach to the analysis of the hydrological data. This method compares catchments of similar size, geology and vegetation cover so as to identify the impacts of the specified land cover changes on affected areas and not some other physical factor. A perusal of the physical characteristics of the catchments detailed in Table 1 suggests a strong similarity between the sizes and physical properties of the catchments of Rocky Valley Creek and Pretty Valley Creek, Rocky Creek and Cope Creek, and the Rocky Valley Stream and Pretty Valley Stream.

	Rocky Valley Creek	Pretty Valley Creek	Cope Creek	Rocky Creek	Rocky Valley Stream	Pretty Valley Stream	East Kiewa River	West Kiewa River
Area (hectares)	1848	2020	227	329	6936	7533	14870	8818
Elevation of highest peak (metres)	1819	1837	1837	1785	1884	1876	1884	1922
Elevation of stream gauge (metres)	1576	1586	1687	1597	694	675	662	713
High Plains topography (%)	100	100	100	100	51	51	51	13
Granodiorite, gneiss and schist geology (%)	76	73	100	99	92	90	91	25
Mossland cover (%)	20	20	13	16	7	7	7	0
Grassland cover (%)	12	41	14	33	5	13	9	2
Heathland cover (%)	50	29	64	41	26	15	20	6
Snowgum woodland cover (%)	18	10	9	10	35	29	32	29
Alpine ash forest cover (%)	0	0	0	0	24	35	29	52
Mixed species forest cover (%)	0	0	0	0	3	1	3	11
Area burnt in 1939 bushfire (%)	65	25	25	25	70	15	48	49
Date of commencement of useable record	June 1925	June 1925	May 1941	May 1940	Aug. 1938	Aug. 1938	Jan. 1926	June 1926
Date of conclusion of useable record	Oct. 1947	Feb. 1959	July 1960	Sept. 1959	Apr. 1959	Apr. 1959	Apr. 1959	Apr. 1981
Mean annual precipitation (mm)	2200	2066	1892	2472	2179	2017		1673
Mean annual streamflow (mm)	1513	1574	1239	2323	1632	1567		1351

Table 1. Physical characteristics of several catchments in the Bogong High Plains area.

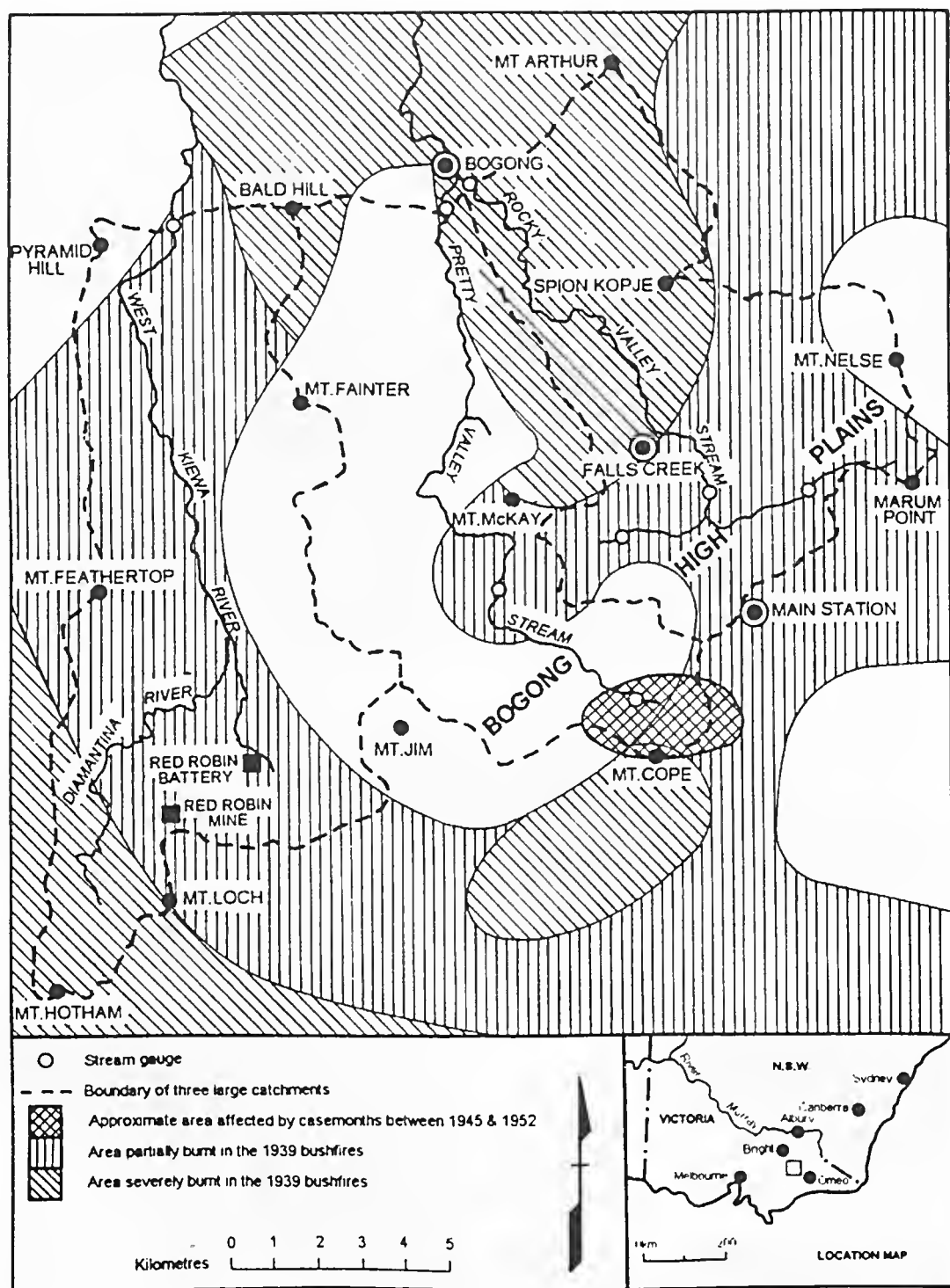


Fig. 1. Location of stream gauges and the distribution of relevant land uses in the corresponding catchments.

However, Table 1 indicates that the catchment of the West Kiewa River differs in geological and vegetation characteristics from the East Kiewa River catchment (and the Rocky Valley and Pretty Valley Stream catchments) making that approach problematic. In addition, the presence of other land uses such as grazing in the elevated sections of the three catchments limits a rigorous pre-versus post-event analysis. In the light of these limitations, it was decided that the use of hydrological modelling was not appropriate in this study. Instead, non-parametric tests have been extensively employed to examine the impacts of land use activities on the hydrology of the catchments in question. The advantage in using non-parametric tests is that they do not make implicit assumptions about the populations from which samples are drawn, and still give rise to exact probability statements (Till 1974; Coshall 1989).

Given the constraints on methods of analysis, it was desired to obtain meaningful data sets from the runoff data available. From the daily runoff record for the three streams, streamflow was separated into baseflow and quickflow using the method adopted by Langford & O'Shaughnessy (1977). Quickflow was defined as storm runoff, and baseflow as the contribution of groundwater to the total runoff. The water year was typically found to start in April, and annual runoff series were adjusted to follow the water year from April to March. Catchment precipitation for the three streams was determined by the Thiessen polygon method using all the available precipitation stations in the area, the most important of which were located at Bogong township, Falls Creek (known as Ropers), the Bogong High Plains (known as Main Station), Mt Hotham (Fig. 1), Harrierville and Smoko. Once the annual and monthly precipitation, streamflow, baseflow and quickflow values for the three streams were known, values for the percentage of precipitation occurring as streamflow, baseflow and quickflow were calculated. These data sets were used extensively in this paper, as they negate the possibility of detecting hydrological change associated with climatic variations such as those identified by Pittock (1975).

The methodology adopted in this study was twofold. Trends in the hydrological data series were identified by use of descriptive techniques and, where an apparent change associated with land cover changes occurred, non-parametric tests were applied to determine the statistical significance of those changes. A hydrograph is a time-series plot of the rise in water above a datum within a streambed in response to a precipitation event. Flow-duration curves are a plot of discharge against

the percentage of time that discharge value is equalled or exceeded, and a steep curve indicates a prompt conversion of precipitation to streamflow (Wilson 1990). Double-mass curves are a plot of two cumulated quantities that produces a straight line plot so long as the data are proportional or a break in slope when the constant of proportionality between the two variables is altered (Searey & Hardison 1960).

Three non-parametric tests have been used in this paper: the Median test, the Mann-Whitney U test, and the Kruskal-Wallis one-way analysis of variance by ranks test. The Median test assesses whether two independent groups of data have been drawn from populations with the same median (Siegel 1956). The Mann-Whitney U test is one of the most powerful non-parametric tests and indicates whether two independent groups of data have been drawn from the same population (Coshall 1989). The Kruskal-Wallis one-way analysis of variance by ranks test determines whether the independent samples are from different populations with respect to the averages (Siegel 1956). Each of these tests operates from the null hypothesis that there are no differences between the data sets tested.

THE 1939 BUSHFIRE

The fires of January 1939 burnt about one-third of the land in Victoria (Noble 1977) and were deliberately lit (Stretton 1939). The Rocky Valley and Pretty Valley Creeks were each burnt in the 1939 fires, but to varying extents. On the basis of eyewitness accounts, post-fire reports, reminiscences, and an extensive number of contemporary photographs, it has been estimated that about 65% of the Rocky Valley Creek catchment were burnt in 1939, and about 25% of the Pretty Valley Stream catchment were affected. Also, about 70% of the Rocky Valley Stream catchment was burnt in 1939, 15% of the Pretty Valley Stream catchment, 48% of the East Kiewa River catchment, and 49% of the West Kiewa River catchment was affected. The catchment of Rocky Valley Stream was the most severely affected area of all the catchments under consideration, and most of the alpine ash and snow gum timber in that catchment were totally burnt. The West Kiewa Valley was only partially burnt, mostly by a ground fire after the main fire front had passed through, leaving large stands of unburnt alpine ash available for later logging. The approximate distribution of areas burned is given in Fig. 1.

The first approach taken to examine the effect of the 1939 bushfire on the streams of the Victorian Alps was to examine the storm hydrographs of those catchments that were burnt. The two-hourly hydrographs of the three watercourses for the month of January are given in Fig. 2. The Rocky Valley Stream hydrograph showed a short duration drop in runoff followed by a marked increase in flow that persisted after the first post-fire precipitation event. The short-term drop in flow occurred during the afternoon of 11 January, which was probably the time when the fires were actively burning in Rocky Valley, and thereafter the Rocky Valley Stream baseflow increased with respect to Pretty Valley Stream and the West Kiewa River. The catchments of Pretty Valley Stream and the West Kiewa River did not show any apparent response to the 1939 fires. In fact, this was the data McArthur (1964) used to claim 'high intensity fire produces an immediate and spectacular increase in streamflow'. However, McArthur (1964) did not subject the streamflow data to any form of

statistical analyses. The same result was not replicated for any of the other catchments examined. Neither the Rocky Valley Creek nor Pretty Valley Creek produced altered storm hydrographs. There were no short, sharp rises in storm hydrographs immediately following the fire similar to that Brown (1972) found at Yarrangobilly in NSW, nor were there any multiple peaks in the severely burnt catchment such as Mackay et al. (1980) found in the Eden area of NSW.

To determine whether the bushfire affected daily streamflow after the first storm event, flow-duration analyses were performed on the Rocky Valley Creek catchment. Four different sets of daily data were plotted, representing the total pre-fire period, the first year after the fires, the first two years after the fires, and the first five years after the fires (Fig. 3). All records showed that the majority of the daily flows for the first year after the fire was consistently higher than those of the thirteen years before the fires. The trend became blurred for low probability, infrequent, storm runoff events,

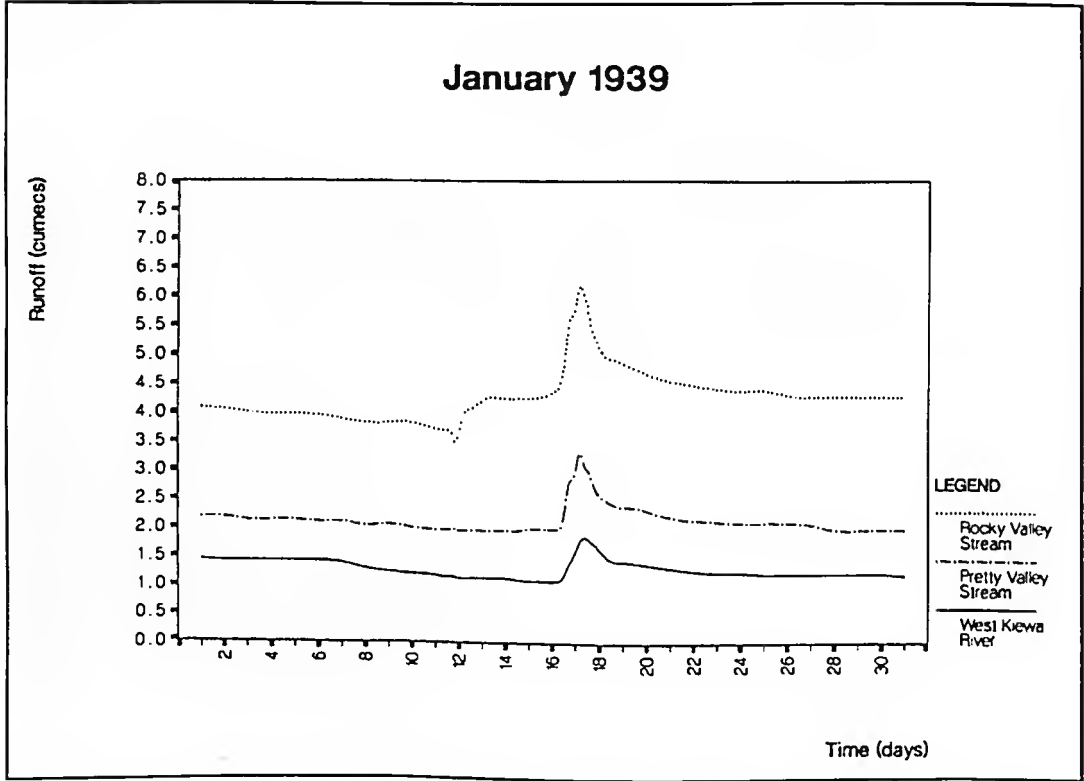


Fig. 2. Two-hourly hydrographs for Rocky Valley Stream, Pretty Valley Stream and the West Kiewa River for January 1939.

but this may have been a function of the fact that daily rather than instantaneous storm hydrographs were used in this analysis. The flow-duration curves indicated that the streamflow increased for the first

year after the fires. Although not shown here, flow-duration curves for the Pretty Valley Creek, East Kiewa River and West Kiewa River produced very similar plots.

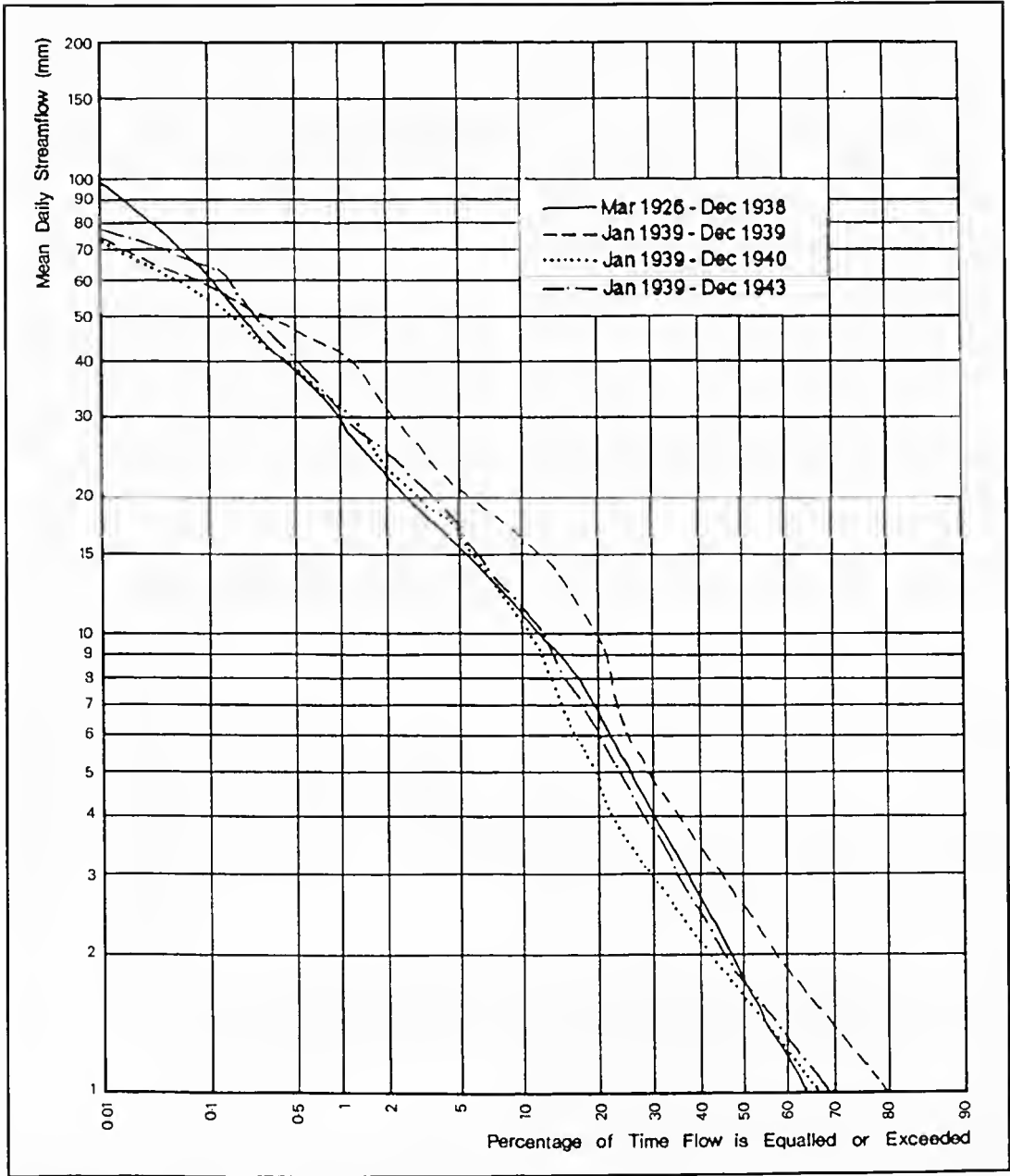


Fig. 3. Flow duration curves of Rocky Valley Creek on the Bogong High Plains for certain periods before and after the 1939 bushfires. About 65% of the catchment of the Rocky Valley Creek was burned by the fire.

As a guard against the possibility that the watercourses examined were all responding to fire similarly, since all catchments were burnt to a certain degree, the Mann-Whitney non-parametric test was applied to the pre- and post-fire hydrological record of four streams (Table 2). The same tests could not be applied to the Rocky Valley Stream and Pretty Valley Stream records because gauges on those rivers were installed less than one year before the fire. Of particular interest are the results of the tests comparing the January 1939 flows to the January flows for the previous thirteen years, the February 1939 flows to those of the previous February flows, etc. In the East Kiewa and/or the West Kiewa River catchments, there was a hint that the flows during the three months immediately after the fires were different from the previous monthly values. However, the data in Table 2 suggests these differences were statistically weak, as the Mann-Whitney test was only significant at the 90% confidence level.

Despite the magnitude of the 1939 bushfires in the Bogong High Plains area, it appears that there were only muted changes in the runoff characteristics of the catchments that were affected by the fires. A small drop in flow of about six hours was observed for Rocky Valley Stream, followed by an increase in baseflow for around 48 hours. No other stream portrayed this phenomenon. Subsequent storm hydrographs for all catchments continued in their pre-fire pattern.

However, streamflow, baseflow and quickflow runoff did increase for the first three months after the fire, although only statistically significant at the 90% confidence level. The daily flows for the first year after the fires were greater than the pre-fire flows in all cases except for large storm events. These results occurred independent of other land uses in the catchment of the West Kiewa River, since the 1939 bushfire predated all logging and mining activities. The effects of the 1939 fires on the runoff of the Bogong High Plains area were not as pronounced as that which was suggested by McArthur (1964), nor as prolonged as that found by Langford (1976) in the *E. regnans* forest in north-central Victoria.

INSECT ATTACK

There have been several occasions when insect plagues have impacted the subalpine vegetation of the Bogong High Plains. Between 1948 and 1952, the grasslands in the vicinity of Mt Cope were impacted by a swiftmoth plague (a species of *Oncopera* belonging to the family Hepialidae). This insect was found to be a very destructive pest of the alpine grasses *Poa australis* on both the Kosciusko plateau and the Bogong High Plains during the late 1940s and early 1950s. Carr & Turner (1959) recorded that 'damage to the aerial parts of the tussocks was slight' but that 'when

Data series	Time period tested	Rocky Valley Creek			Pretty Valley Creek			East Kiewa River			West Kiewa River		
		sf	bf	qf	sf	bf	qf	sf	bf	qf	sf	bf	qf
Monthly data (% of pptn)	June 1926-Dec. 1938 vs Jan. 1939-Dec. 1939	-	-	-	-	-	-	-	-	-	#	-	##
	June 1926-Dec. 1938 vs Jan. 1939-Dec. 1940	-	-	-	-	-	-	-	-	-	-	-	-
	June 1926-Dec. 1938 vs Jan. 1939-Dec. 1943	-	-	-	-	-	-	-	-	-	-	-	-
January data (% of pptn)	Jan. 1927-Jan. 1938 vs Jan. 1939	-	-	-	-	-	-	#	#	-	#	#	-
	Jan. 1927-Jan. 1938 vs Jan. 1939-Jan. 1940	-	-	-	-	-	-	-	-	-	-	-	-
	Jan. 1927-Jan. 1938 vs Jan. 1939-Jan. 1943	-	-	-	-	-	-	-	-	-	-	-	-
February data (% of pptn)	Feb. 1927-Feb. 1938 vs Feb. 1939	-	-	-	-	-	-	-	#	-	-	#	#
	Feb. 1927-Feb. 1938 vs Feb. 1939-Feb. 1940	-	-	-	-	-	-	-	-	-	-	-	-
	Feb. 1927-Feb. 1938 vs Feb. 1939-Feb. 1943	-	-	-	-	-	-	-	-	-	-	-	-
March data (% of pptn)	Mar. 1927-Mar. 1938 vs Mar. 1939	-	#	-	-	-	-	-	#	-	-	-	-
	Mar. 1927-Mar. 1938 vs Mar. 1939-Mar. 1940	-	-	-	-	-	-	-	-	-	-	-	-
	Mar. 1927-Mar. 1938 vs Mar. 1939-Mar. 1943	-	-	-	-	-	-	-	-	-	-	-	-

Table 2. The results of the Mann-Whitney test to determine the effects of the 1939 bushfire on the hydrological properties of four catchments. sf = streamflow; hf = baseflow; qf = quickflow; ## = significant at the 95% confidence level; # = significant at the 90% confidence level; - = not significant.

the dead grass was pulled away, long tubular galleries made of pieces of grass leaves cemented together with silk were found here and there at the bases of the tussocks'. Carr & Turner (1959) noted that the distribution of swiftmoth damage both coincided with the areas burnt in the 1939 fires, and appeared to reach its maximum in 1952. Grassland communities beneath snowgums were also affected. The area that was severely damaged 'on the northern slopes of Mt Cope' coincided with the Cope Creek catchment at a time when the stream gauge was in operation (Table 1). Table 1 indicates that 33% of the vegetation cover in the Cope Creek catchment is grassland and 10% is covered by snow gum woodlands, giving a total of 43% of the catchment that may have been affected by the swiftmoth plague.

Double-mass curves of Cope Creek monthly streamflow values were plotted against those of a nearby unaffected catchment, the Rocky Creek

(Fig. 1). The plot of two cumulated quantities produces a straight line plot so long as the data are proportional, but if a break in slope is evident then a change in the constant of proportionality between the two variables has occurred. The results shown in Fig. 4 suggest that relative to the unaffected Rocky Creek runoff, Cope Creek runoff increased for a period of about five years after the swiftmoth plague occurred. Although not shown in Fig. 4, plots of baseflow and quickflow runoff for Cope Creek compared to Rocky Creek produced similar results. The initial break in the double-mass curve was found to occur in January 1951.

In order to determine whether this break was statistically significant or not, the Mann-Whitney U test was applied to both the Cope Creek data. The hydrological record of the Cope Creek catchment was divided into two parts, and the period of record from May 1941 to December 1950 was compared to that of January 1951 to July 1960.

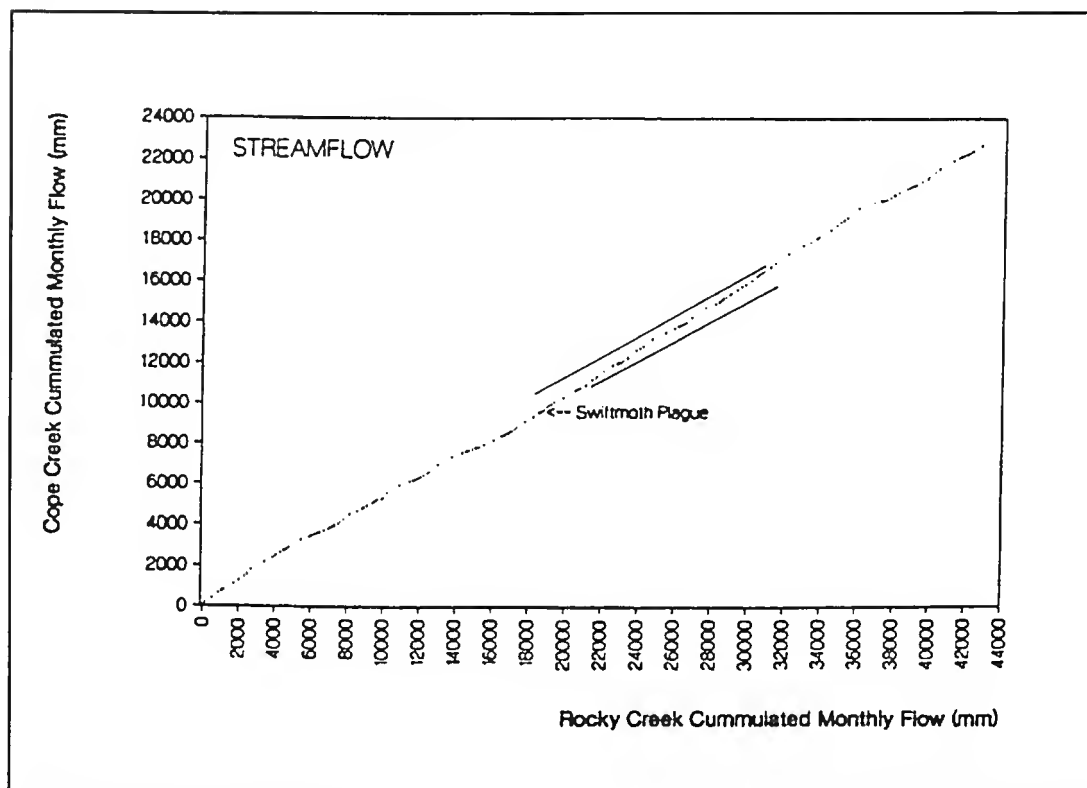


Fig. 4. Double-mass curve of Cope Creek and Rocky Creek monthly runoff depicting the hydrological impact of a swiftmoth plague that lasted for about five years.

The proportion of precipitation occurring as streamflow, baseflow and quickflow on both an annual and monthly basis were subjected to the non-parametric test. It was found that the annual proportion of precipitation occurring as quickflow data prior to 1951 displayed a different statistical distribution to the corresponding data after 1951. This change was significant at the 95% confidence level.

The double-mass curve indicates that the period of time that the hydrological conditions of the Cope Creek catchment were altered was about six to seven years (Fig. 4). The Victorian Interim Reference Advisory Committee (1977) estimated that the snowgrass species *Poa australis* would take between five and ten years to recover its full floristic potential following fire. Given that Carr & Turner (1959) observed that the swiftmoths targeted those areas that had been burnt in the 1939 fires, it seems reasonable to suggest that by 1951 the grasslands had reached full floristic recovery from the fires, and that this was the attraction by the swiftmoths. It also may be inferred from these results that the time taken for the grasslands to recover hydrologically from the insect plague was shorter than that necessary for floristic recovery.

MINING OPERATIONS AT THE RED ROBIN MINE

Although mining has been a significant land use in the Mt Hotham region since the early 1850s, a minor mining sensation occurred during the early 1940s when a local identity named William Spargo discovered rich gold just north of Mt Loeh (Fig. 1). Three reefs were discovered and they became collectively known as the Red Robin Mine (Kenny 1941). In his first year of mining, Spargo extracted 6690 grams of gold from two tonnes of ore: a result that drew much attention to the area. Between November 1940 and January 1942, twenty leases covering an area of more than 350 hectares were pegged around the Red Robin Mine, as lease owners engaged in extensive exploration work and loaming. However, World War II intervened, and very little work was done between June 1942 and November 1945. Between 1945 and 1964, the ownership and management of the Red Robin Mine changed a number of times. During this time, a road from Mt Hotham to the mine was constructed, a three-head stamp battery was erected at the mine, an average of 315 grams of gold per tonne of ore was returned, a second battery on the West

Kiewa River three kilometres to the northeast was constructed, and interest in the surrounding area waned.

In November 1964 the leases covering the Red Robin reefs were acquired by the Livingstone brothers (millionaires of yachting fame from London), and a new company 'R. R. Mining Co. Pty. Ltd.' was formed. A period of intense activity and high production efforts followed. During 1966 the mine was kept in operation throughout the entire year, necessitating the continual clearing of snow from the roads and mine area. Ten men were employed to mine enough ore to enable the battery to run continuously, and a new set of living quarters was constructed to house the employees. Although more than 28 800 grams of gold were extracted, the ratio of gold to ore was only 23 grams per tonne and the mine was not financially viable. Between 1969 and the death of John Livingstone in 1977 very little work was done at the mine even though extensive exploratory drilling was carried out between 1968 and 1970. In June 1978 the ownership of the mine was transferred from the Livingstone Estate to previous owners, the Harris family, who have operated the mine continuously since then.

There were five main phases of mining in the area surrounding the Red Robin Mine. The first occurred immediately after the discovery of the Red Robin Reef in late 1940 and lasted until 1942. The second phase extended from 1945 to 1964, with most of the activity occurring during the late 1940s. The third phase was typified by the entrepreneurial operation of the Red Robin Mine, and centred around the 1965 to 1968 period. The fourth phase of mining activity took place between 1968 and 1970 when more than 600 hectares of exploration leases were held in the Hotham Heights area but no major finds eventuated as a result. The final phase of mining in the Hotham Heights area extended from 1980 to the present when only the leases for the Red Robin Mine were valid and the mine was worked consistently and economically by Ken Harris. Given that the Red Robin Reef is located in the headwaters of the West Kiewa River, each of the five phases of mining is now investigated by examining the hydrological record of the West Kiewa River. Logging activities have also taken place in the West Kiewa valley during the later three phases of mining, but Lawrence (1990) demonstrated that the areal extent of those activities each year was too small to produce statistically significant hydrological changes.

The hydrological record of the West Kiewa River was divided into pre-mining, mining, and post-mining periods for the five phases of mining

under consideration. The Median and Kruskal-Wallis non-parametric tests were applied to this data as these tests allowed for a comparison of three sequential data sets. When the November 1940 to June 1942 period was compared to the entire record, and the two non-parametric tests were applied to determine if the three time periods demonstrated statistically significant runoff characteristics, no significant results were obtained (Table 3). Likewise, a comparison of the November 1945 to June 1950 period to the entire record did not render the three data sets significantly different to each other. The fourth and fifth periods of mining activity also gave statistically insignificant results. In all of those cases, the percentage of precipitation occurring as streamflow, baseflow and quickflow of the pre-mining, mining, and post-mining eras suggested that mining operations during the 1940s, 1970s and 1980s did not cause any change in the hydrological behaviour of the West Kiewa River with respect to the entire hydrological record.

In contrast to the minimal hydrological impact of the first, second, fourth, and fifth phases of mining, the operation of the Red Robin Mine by the Livingstone brothers during the mid 1960s

resulted in marked changes to the runoff from the West Kiewa River. When the two non-parametric tests were used to compare the 1964/65–1968/69 period to the entire West Kiewa River runoff record, statistically significant differences in annual runoff were found. In addition, the monthly West Kiewa River data for the November 1964 to January 1968 period was significantly different from both the pre- and post-mining era data (Table 3). The mean monthly streamflow, baseflow and quickflow values have been plotted in Fig. 5. The difference between the mining and non-mining data is striking, given that the seasonal distribution of the pre- and post-mining runoff patterns were almost identical. The mean streamflow and baseflow values for each month between January and November were always lower during the mining era of the mid 1960s with respect to the other time periods (particularly between April and November) and the December values were higher. The mean quickflow values for each month between January and June were also lower during the mining period than at any other time, but were similar to that of the non-mining periods between August and December. These results stand independent of the impacts of forestry on runoff.

Time period tested	Data series tested	Med.	K-W
1927/28–1939/40 <i>vs</i>	Percentage of precipitation occurring as streamflow	–	–
1940/41–1942/43 <i>vs</i>	Percentage of precipitation occurring as baseflow	–	–
1943/44–1980/81	Percentage of precipitation occurring as quickflow	–	–
1927/28–1944/45 <i>vs</i>	Percentage of precipitation occurring as streamflow	–	–
1945/46–1950/51 <i>vs</i>	Percentage of precipitation occurring as baseflow	–	–
1951/52–1980/81	Percentage of precipitation occurring as quickflow	–	–
1927/28–1963/64 <i>vs</i>	Percentage of precipitation occurring as streamflow	–	–
1964/65–1968/69 <i>vs</i>	Percentage of precipitation occurring as baseflow	##	#
1969/70–1980/81	Percentage of precipitation occurring as quickflow	–	–
June 1926–Oct. 1964 <i>vs</i>	Monthly streamflow	#	###
Nov. 1964–June 1968 <i>vs</i>	Monthly baseflow	#	###
July 1968–Apr. 1981	Monthly quickflow	–	–
1927/28–1966/67 <i>vs</i>	Percentage of precipitation occurring as streamflow	–	–
1967/68–1969/70 <i>vs</i>	Percentage of precipitation occurring as baseflow	–	–
1970/71–1980/81	Percentage of precipitation occurring as quickflow	–	–
1927/28–1978/79	Percentage of precipitation occurring as streamflow	–	–
<i>vs</i>	Percentage of precipitation occurring as baseflow	–	–
1979/80–1980/81	Percentage of precipitation occurring as quickflow	–	–

Table 3. The results of non-parametric tests applied to determine the effects of mining operations on the hydrological properties of the West Kiewa River. Med. = Median test; K-W = Kruskal-Wallis test; ### = significant at the 99% confidence level; ## = significant at the 95% confidence level; # = significant at the 90% confidence level; – = not significant.

These results suggest three ways in which the runoff from the West Kiewa River was affected by the mining activities of the mid 1960s. Firstly, there was a significant reduction in the runoff of the West Kiewa River due to the quantity of water used in the operation of the Red Robin Mine battery. The low streamflow values were not entirely due to low precipitation values, as there was no statistically significant difference between the precipitation of the three periods. Secondly, all months of the year except December experienced a reduction in streamflow during the 1960s, suggesting that there was a consistent withdrawal of water from the West Kiewa River to run the crushing battery at that time. Thirdly, the mean monthly quickflow values for August to December indicate that, although the total streamflow values for the mid 1960s period were low, that more streamflow occurred as quickflow than was normal for the West Kiewa River. This was probably associated with the sporadic release of water from the battery back to the river at the time of crushing.

In the examination of the effects of mining on the hydrological properties of the West Kiewa River the following conclusions may be reached. Between November 1940 and June 1942, when the Red Robin Mine was in its infancy and twenty other leaseholders were prospecting in the surrounding areas, there were no changes in the hydrological record in comparison to the 1927 to 1981 period. After World War II, when the Red Robin Reef was again worked and the surrounding areas prospected and loamed, it was also found that the total runoff between November 1945 and June 1950 did not change significantly. Between November 1964 and January 1968, when the Livingstone brothers owned the Red Robin Mine, the streamflows and baseflows of the West Kiewa River were lower for all months of the year except December. This statistically significant result implies that more water was being used in the operation of the battery during those years in comparison to the non-mining eras. On this basis, it can be concluded that reef mining and the non-stop operation of a battery in

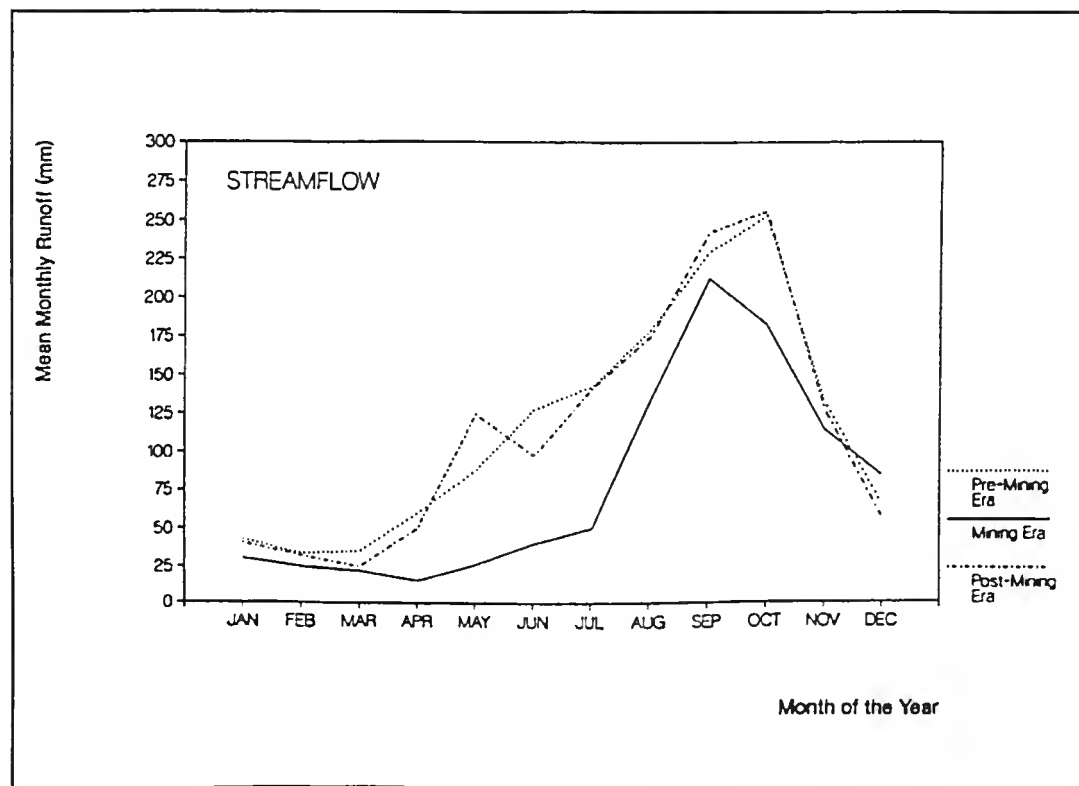


Fig. 5. Mean monthly runoff values for three time periods centering around the mining activity in the West Kiewa Valley during the mid 1960s.

the West Kiewa Valley altered the seasonal spread and quantity of runoff in the West Kiewa River. The phase of extensive exploration in the Hotham Heights area between 1968 and 1970, and the small-scale operations of the Red Robin Mine from 1980 to the present have had an insignificant impact on the hydrology of the West Kiewa River.

HYDROLOGICAL SUSTAINABILITY

The three examples of changes in land cover in the subalpine area of the Victorian Alps considered here each resulted in a hydrological alteration. The effect of the 1939 bushfire on the streamflow of various creeks was evident for a year following the event, whereas both the swiftmoth plague in the Mount Cope area and intensive mining activity in the West Kiewa Valley produced hydrological changes over a five year period. All three examples considered were discrete events occurring over a short period of time. Other land use activities such as construction of the Kiewa Hydro-Electric Scheme and grazing activities on the subalpine pastures occur over a much longer time frame and have been shown elsewhere to produce long-term hydrological changes (Lawrence 1995).

There is a mounting body of evidence to suggest that the majority of the damage to the Bogong High Plains pre-dated the time period examined in this paper (Lawrence 1994). Several decades of relatively low precipitation and heavy grazing activities at the start of this century resulted in pronounced vegetation changes in the subalpine environment of the area (Lawrence, this volume). If the hydrological response to those land cover changes could have been quantified, significant alterations to the streamflow record would have resulted. The fact that bushfire, insect attack and mining activities between the late 1930s and mid 1960s registered elevated runoff above pre-existing values suggests that the damaging land use activities prior to that time would have produced more pronounced hydrological changes.

Given that the Australian Alps are such an important area for water production on a national scale, any activity that produces a change in land cover should be minimised in order to achieve hydrological sustainability. Some may argue that because the alpine area is such an important water producing area that land cover changes which result in increased runoff should be encouraged. However, it must be remembered that land use activities such as bushfires, grazing, insect attack, mining, etc. result in vegetation destruction and erosion that in turn results in more particulate

matter finding its way into the stream waters. Greater runoff values from land cover changes is almost always associated with a decline in water quality. The recognition that land management strategies in the Australian Alps were sometimes inappropriate in the past should result in management options that will produce hydrological sustainability today.

REFERENCES

- AUSTRALIAN ACADEMY OF SCIENCE, 1957. *Report on the conditions of high mountain catchments of New South Wales and Victoria*. Australian Academy of Science, Canberra.
- BEAVIS, F. C., 1962. The geology of the Kiewa area. *Proceedings of the Royal Society of Victoria* 75: 349–410.
- BETHLAHMY, N., 1974. More streamflow after a bark beetle epidemic. *Journal of Hydrology* 23: 185–189.
- BROWN, J. A. H., 1972. Hydrologic effects of a bushfire in a catchment in southeastern New South Wales. *Journal of Hydrology* 15: 77–96.
- BROWN, J. A. H., 1983. *Water 2000: Consultants Report No. 1: Australia's surface water resources*. Australian Government Publishing Service, Canberra.
- CARR, S. G. M. & TURNER, J. S., 1959. The ecology of the Bogong High Plains. I. The environmental factors and the grassland communities. *Australian Journal of Botany* 7: 12–33.
- COMMONWEALTH OF AUSTRALIA, 1996. *Australia: state of the environment 1996*. CSIRO, Melbourne.
- COSHALL, J., 1989. *The application of nonparametric statistical tests in geography: Concepts and Techniques in Modern Geography* No. 50.
- COSTIN, A. B., 1957. *High mountain catchments in Victoria in relation to land use*. Soil Conservation Authority, Melbourne.
- COSTIN, A. B., WIMBUSH, D. J., KERR, D. & GAY, L. W., 1959. *Studies in catchment hydrology in the Australian Alps: 1: Trends in soil and vegetation*. CSIRO Division of Plant Industry Technical Paper 13.
- CRABB, P., 1997. *Murray–Darling Basin Resources*. The Murray–Darling Basin Commission, Canberra.
- FLOOD, J., 1980. *The moth hunters: Aboriginal prehistory of the Australian Alps*. Australian Institute of Aboriginal Studies, Canberra.
- FLUIN, J., 1995. *Degradation of alpine streams: the ecological effects of sewage discharge on the alpine aquatic environment*. Unpublished BA(Hons) Thesis, Department of Geography, University of Adelaide.
- JAYASURIYA, M. D. A., DUNN, G., BENYON, R. & O'SHAUGHNESSY, P. J., 1993. Some factors affecting water yield from mountain ash (*Eucalyptus regnans*) dominated forests in southeast Australia. *Journal of Hydrology* 150: 345–367.

- KENNY, J. P. L., 1941. Red Robin and One Alone Reefs, Illoham Heights. *Mining & Geology Journal of Victoria* 2: 263-267.
- KIRKPATRICK, J., 1994. *A continent transformed: human impact on the natural vegetation of Australia*. Oxford University Press, Melbourne.
- KUCZERA, G., 1987. Prediction of water yield reductions in ash-mixed species eucalypt forests. *Journal of Hydrology* 94: 215-236.
- KULIK, V., 1990. Bushfire hydrology: runoff as an indicator of critical fire danger. *Water Resources Development* 6: 44-54.
- LANGFORD, K. J., 1976. Change in yield of water following a bushfire in a forest of *Eucalyptus regnans*. *Journal of Hydrology* 49: 87-114.
- LANGFORD, K. J. & O'SHAUGHNESSY, P. J., eds, 1977. *First progress report. North Maroondah*. Melbourne and Metropolitan Board of Works, Water Supply Catchment Hydrological Research Report No. MMBW-W-0005.
- LAWRENCE, R. E., 1990. *The interaction between the environment, land use and hydrology of the Bogong High Plains Area from 1850 to 1985*. Unpublished PhD Thesis, Department of Geography, University of Melbourne.
- LAWRENCE, R. E., 1994. Environmental changes on the Bogong High Plains, 1850s to 1990s. In *Australian environmental history: Essays and cases*, S. Dovers, ed., Oxford University Press, Melbourne, 167-197.
- LAWRENCE, R. E., 1995. The effects of grazing activity on the hydrology of the Bogong High Plains, Australia. *The Rangeland Journal* 17: 138-153.
- LOH, I. C., HOOKEY, G. R. & BARRETT, K. L., 1984. *The effect of bauxite mining on the forest hydrology of the Darling Range, Western Australia*. Water Resources Branch Report WRB 73, Public Works Department, Western Australia.
- LOVE, L. D., 1955. The effect on streamflow of the killing of spruce and pine by the Engelmann spruce beetle. *Transactions of the American Geophysical Union* 36: 113-118.
- MACKAY, S. M., MITCHELL, P. A. & YOUNG, P. C., 1980. Hydrologic changes after wildfire in small catchments near Eden, NSW. In *Hydrology & Water Resources Symposium, 1980, Adelaide*. Institute of Engineers, Australia, National Conference Publication 80/9, 150-156.
- MCCARTHUR, A. G., 1964. Streamflow characteristics of forested catchments. *Australian Forester* 28: 106-118.
- MCDougALL, K., 1982. *The alpine vegetation of the Bogong High Plains*. Ministry for Conservation (Melbourne), Environmental Studies Publication 357.
- MCDougALL, K. L. 1989. *The effect of excluding cattle from a mossbed on the Bogong High Plains, Victoria*. Arthur Rylah Institute for Environmental Research, Technical Report Series 95. Department of Conservation, Forests & Lands, Victoria.
- McMAHON, T. A., FINLAYSON, B. L., HAINES, A. T. & SRIKANTHAN, R., 1992. *Global runoff: continental comparisons of annual flows and peak discharges*. Catena Verlag, Cremlingen-Destedt.
- NONLE, W. S., 1977. *Ordeal by fire: the week a state burned up*. Hawthorn Press, Melbourne.
- PITTOCK, A. B., 1975. Climatic change and patterns of variation in Australian rainfall. *Search* 6: 498-504.
- ROWE, R. K., 1972. *A study of the land in the catchment of the Kiewa River*. Soil Conservation Authority, Melbourne.
- RUPRECHT, J. K., 1991. Hydrologic impact of bauxite mining and rehabilitation in southwest Western Australia. *International Hydrology and Water Resources Symposium*. Institute of Engineers, Australia, National Conference Publication 91/22: 381-385.
- SEARCY, J. K. & HARDISON, C. H., 1960. Double mass curves. In *Manual of hydrology: Part I. General surface-water techniques*. United States Geological Survey Water Supply Paper, 1541-B.
- SIEGEL, S., 1956. *Non-parametric statistics for the behavioural sciences*. McGraw-Hill, New York.
- SLATTERY, D., 1998. *The Australian alps: Kosciuszko, Alpine and Namadgi National Parks*. University of New South Wales Press, Sydney.
- STREITON, L. E. B., 1939. *Report of the Royal Commission to inquire into the causes of and measures taken to prevent the bushfires of January, 1939, and to protect life and property and the measures to be taken to prevent bushfires in Victoria and to protect life and property in the event of future bushfires*. Parliamentary Paper 6912/39. Government Printer, Melbourne.
- TILL, R., 1974. *Statistical methods for the earth scientist: an introduction*. Macmillan, London.
- VICTORIA, INTERIM REFERENCE AREAS ADVISORY COMMITTEE, 1977. *Estimates of time required for recovery of Victorian plant communities from crown and grass fires*. Land Conservation Council, Melbourne.
- WAHREN, C.-H. A., PAPST, W. A. & WILLIAMS, R. J., 1994. Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: an analysis of records from 1945 to 1994. *Australian Journal of Botany* 42: 608-612.
- WILLIAMS, R. J. & ASHTON, D. H., 1987. Effects of disturbance and grazing by cattle on the dynamics of heathland and grassland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* 35: 413-431.
- WILSON, E. M., 1990. *Engineering hydrology*, 4th edn. Macmillan, London.

VEGETATION REGENERATION IN A SMALL CATCHMENT ON THE BOGONG HIGH PLAINS, VICTORIA

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Catchment-scale changes to the vegetation communities in a small catchment of the Bogong High Plains of Victoria were investigated for the period from 1961 to 1994. Vegetation changes in four major vegetation communities were inferred from large-scale, panchromatic, aerial photographs from three eras that were analysed by use of a Geographic Information System. Vegetation extent of the snow gum woodland, heathland and mossland increased during this period and there was a concurrent decrease in the extent of grassland/herbfield. Change in the coverage of the vegetation communities also altered between the 1960s and 1990s. The fragmentation of all communities decreased over time. These results suggested an amelioration of the catchment's vegetation that generally accord with the results of plot studies.

Summer grazing of livestock occurred on the Bogong High Plains of Victoria from as early as 1866 (Cabena 1980). Severe degradation of the area's soils and vegetation resulted from the exploitative grazing practices (Costin 1957; Costin 1958; Ashton & Williams 1989) and this degradation climaxed following the severe bushfires of both 1926 and 1939. Measures that included both fire and grazing restrictions were thus implemented from the middle of this century to limit further degradation (Australian Alps Liaison Committee 1992).

In response to this degradation occurring on the Bogong High Plains, two grazed and ungrazed experimental plots were established at Rocky Valley and Pretty Valley in the mid 1940s by the Melbourne University School of Botany. Several other plots were established for particular research projects since the late 1970s, and a number of sites are monitored as part of ongoing research into the effects of grazing (Victoria, Department of Conservation and Environment 1992; Van Rees et al. 1984). Vegetation changes that have occurred on the Bogong High Plains of Victoria in response to decreased grazing pressure and post-fire regeneration have been intensively studied for these small, plot-scale areas. Most of the ecological studies based on information obtained from these plots and from other small-scale areas have established linkages between changes to vegetation and livestock activities and fire.

For the purposes of this study, four broad vegetation communities were examined: snow gum woodland, grassland/herbfield, heathland and

mossland. These were defined as an amalgam of the specific communities identified by McDougall (1982). Of these communities, previous studies have found that snowgum woodlands appear to have been the least affected by grazing. However, selective grazing and the production of bare ground have favoured the growth of shrubs in the understorey (Costin 1958). In comparison, much of the snow gum woodland on the Bogong High Plains shows modification due to the 1926 and 1939 fires. Although snow gum regrowth has attained original height, age of stands has been reduced and appearance is scrubby (Ashton & Williams 1989). Studies such as those by McDougall (1982), Williams & Ashton (1987) and Wahren et al. (1994) found that a succession sequence from grassland to heathland occurred following a disturbance factor such as fire or grazing. In the absence of the disturbance factor, a regenerative process occurred whereby the shrubs senesced over a 50 to 60 year period and were gradually succeeded by climax grassland. The mossland areas have also been observed, both internal and external to the plots, and a cycle of regeneration following damage, established. It was found that cattle, which used the mossbeds as a source of drinking water, were damaging the mossbeds primarily through trampling (Costin 1954; Carr & Turner 1959; Australian Alps Liaison Committee 1992). Destruction of some of the mossbeds also occurred during the 1926 and 1936 bushfires (Lawrence 1998). However, during the past few decades, both the extent and condition of observed mosslands have improved (Ashton & Williams 1989).

The regenerative responses of the subalpine and alpine vegetation on the larger, catchment-scale has received little attention. Are the processes that occur at plot-scale also occurring on a larger scale? If so, is an efficient method of detecting such change possible?

METHODOLOGY

Technique chosen

In order to determine whether or not the regenerative processes were operating at catchment scale, a practical, precise, reliable and relatively cheap method of determining the actual processes on a larger scale was sought. Considering the wealth of relatively large-scale (about 1:10 000), panchromatic, aerial photography that was available for the Bogong High Plains area across several decades, it was decided to interpret vegetation changes from these images within the ARC/INFO geographical information system (G.I.S.). The G.I.S. held many advantages over traditional, manual methods of aerial photography analysis. First, the use of a 'zoom' function allowed magnification of specified indistinct areas, aiding identification of separate vegetation communities and hence precision of boundary discrimination during the process of digitisation. Use of a G.I.S. also allowed easy extrapolation of accurate areal measurements of the different communities, and the output of tailored map displays which could easily communicate the derived information.

Study area

A representative catchment was chosen for which the changing vegetation conditions would be determined. Of the several catchments of the Bogong High Plains, Watchbed Creek catchment was selected for the following reasons: its landuse history was well documented and similar to those of the other catchments of the Plains (Lawrence 1990), all four vegetation communities were represented within the catchment, and previous work by Lawrence (1995) had demonstrated declining runoff from the catchment since the mid 1940s to at least the early 1980s. The declines both in streamflow and quickflow determined during this 42-year period correlated with declining grazing pressure and suggested that the catchment condition was improving.

Watchbed Creek catchment is situated to the south of Mt Nelse on the Bogong High Plains (36°54' latitude, 147°20' longitude) and covers an area of about 305 hectares. The topography of the

catchment is characterised by the gentle undulations of the plateau and Rowe's (1972) derived description suggests that the soils are predominantly shallow organic loams, with undifferentiated stony loams commonly occurring on ridgetops and peats in valleys. Heathland vegetation dominates the catchment, covering almost half the area. The main environmental impacts on the catchment have been due both to the 1926 and 1939 bushfires and to cattle (Lawrence 1990). From maximum stocking rates of about 0.61 head of cattle per hectare in 1952, the intensity of cattle grazing generally decreased from the middle of this century until 1991, after which cattle were eliminated (Bruce 1996).

Aerial photography processes

Of the large archive of aerial photography available for the Watchbed Creek catchment, photographs for three separate eras (1961, 1980 and 1994) were chosen which satisfied six essential criteria. These criteria ensured that the chosen photographs were readily available, of suitable scale (no more than 1:20 000), of adequate and comparable quality (in terms of contrast, focus and resolution), accurate (as determined from ground-truthing), pertained to eras when the precipitation characteristics of the years immediately preceding were comparable and not unusual, and taken at a similar time of both year and day. Each of the four vegetation communities was readily identifiable and easily discriminated from each other for each era selected. The photographs used were all black-and-white panchromatic.

A process of orthorectification for each photograph followed which was required to remove all distortion due to camera obliquity and terrain relief. Elimination of these distorting effects within a Digital Photogrammetric Workstation therefore resulted in the production of three digital orthophotos that, being map-accurate, allowed direct measurement of accurate size and extent from the image. As results from this project relied on accurate areal measurements, such a procedure was essential.

G.I.S. processes

The digital photos resulting from this orthorectification procedure were then imported into an ARC/INFO G.I.S. on a Silicon Graphics workstation for G.I.S. processing and analysis. After delineation of the Watchbed Creek catchment boundary from one image and overlaying of this standard boundary onto the remaining two images,

a process of vegetation community delineation occurred for each orthophoto. The establishment of these boundaries was aided by visual inspection of the original, hard copy photographs, identification of the communities as determined by ground truthing, and inspection of an ancillary 1:15 000 vegetation map. The majority of the clumps of the different communities were found to be quite distinct on the orthophotos, and so delineation proved to be relatively easy.

From the previous process of delineation, it was then possible to extract information from the G.I.S. to determine both the changes in areal extent between the different communities for each of the

eras, and the change in the number of 'clumps' of the vegetation communities. An analysis of both of these measurements would provide an indication of both the nature and rate of change of vegetational regeneration.

RESULTS AND DISCUSSION

An increase in the covers of snow gum woodland (470 709 m² to 565 151 m²), heathland (1 555 267 m² to 1 734 373 m²) and mossland (452 813 m² to 496 108 m²) was apparent between 1961 and 1994 (Fig. 1). This corresponded with a significant

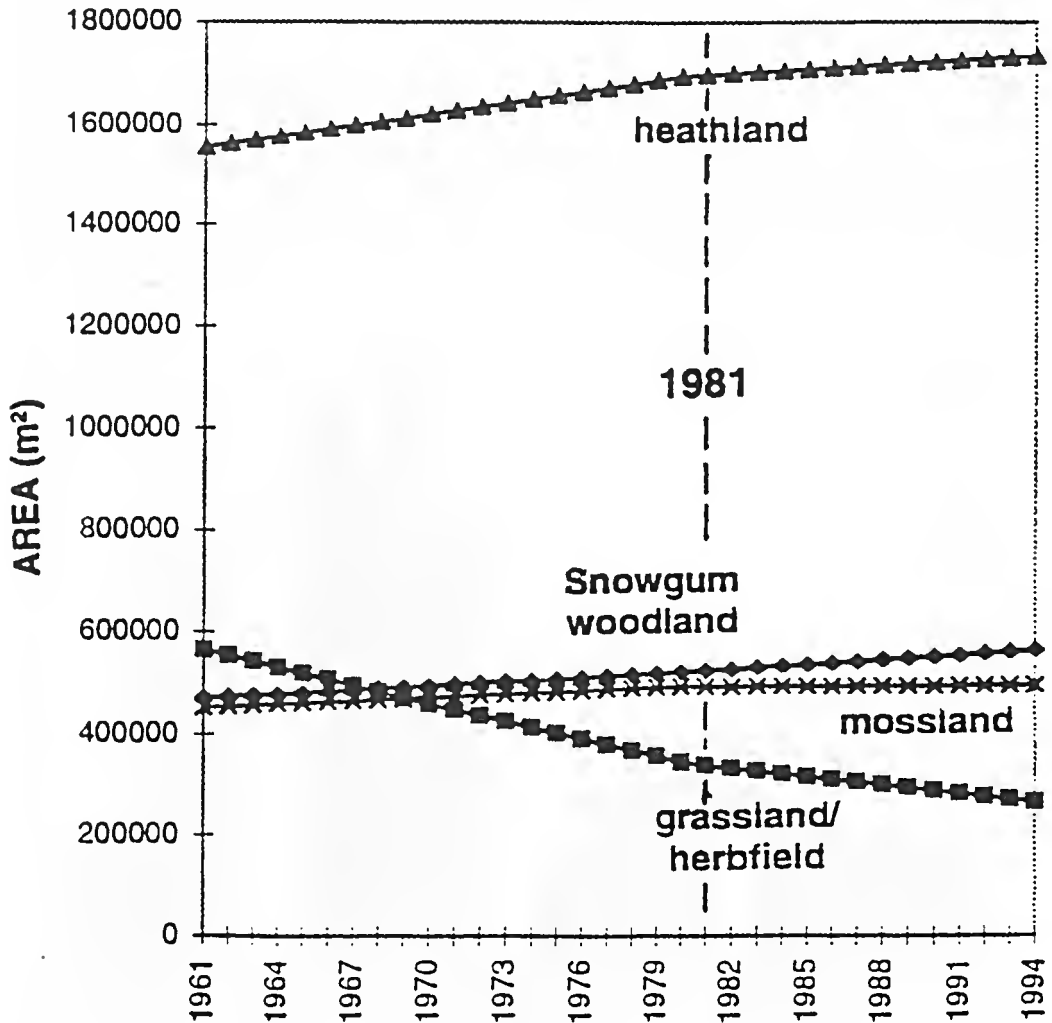


Fig. 1. Trends in the coverage of four major vegetation communities in the Watchbed Creek catchment between the early 1960s and mid 1990s.

decrease in the cover of grassland/herbfield to less than half the coverage present in 1961 ($565\,318\text{ m}^2$ to $265\,554\text{ m}^2$). The changed coverages of the communities were also found to have altered over time (Fig. 2). Thus, the rate of grassland/herbfield decline was found to be decreasing, as was the rate of both heathland and mossland increase. In contrast, the rate of growth in snow gum extent increased between 1980 and 1994 relative to the period from 1961 to 1980. Notable changes to the number of vegetation clumps identified in each era were also found to have occurred (Fig. 3). Continual declining trends were evident for all of the vegetation clumps between 1961 and 1994.

The results of the catchment-wide study generally concurred with the nature of alpine vegetation regeneration as determined from the previous smaller, plot- and point-scale studies. Mossland increased in extent in accordance with the observations of Ashton & Williams (1989), Carr (1977) and McDougall (1989), who attributed expansion to *Sphagnum* growth. Also, woodland area in the Watchbed Creek catchment increased in a manner similar to that discussed by Ashton & Williams (1989). However, although Ashton

& Williams (1989) noted an increase for about 30 years after fire due to vegetative and seed regeneration (which in the present study would have corresponded with an increase to about 1970 after the 1939 fires), the woodland in Watchbed Creek catchment increased to at least 1994.

The decline in extent of grassland/herbfield and concurrent rise in the coverage of heathland agreed with the 30 to 50 year vegetation transition noted by many researchers (eg. McDougall 1982; Williams & Ashton 1987; Williams 1991; Wahren et al. 1994). The declining rates of change observed in the present study for these two communities indicated that the transition from grassland/herbfield to heathland is slowing and that the reconversion to the original, climax grassland may happen in the near future.

The decreasing fragmentation of the vegetation communities is also indicative of a regenerating environment, and is supported by observations of Williams & Ashton (1987), Van Rees et al. (1984), Williams (1991) and others. These authors noted decreases in the amount of bare soil following elimination of cattle from exclusion plots in Rocky Valley and Pretty Valley. It can reasonably be assumed that a decrease in bare soil accompanied

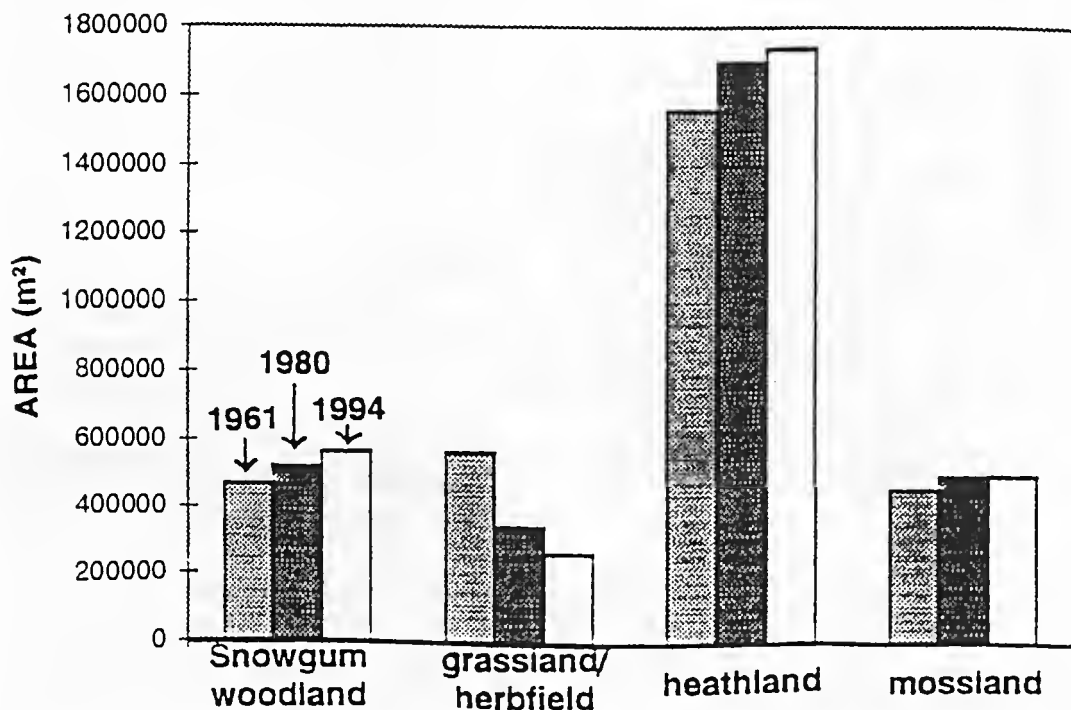


Fig. 2. Changes in areal extent of vegetation communities in the Watchbed Creek catchment over time.

the decreased fragmentation of the vegetation communities observed in the current study. Carr (1977) and McDougall (1989) also noted that ungrazed mossbeds were larger and less fragmented after cattle exclusion due to perimeter enlargement and concealment of drainage lines.

CONCLUSION

The changes to both the areal extent of the vegetation communities and incidence of clumps observed between the three eras therefore generally concurred with published research. These changes suggested that the condition of the vegetation in Watchbed Creek catchment was improving between 1961 and 1994. The improving vegetation condition was attributed to a number of factors, mainly to the implementation of catchment management measures from the mid 1940s. Vegetation changes were therefore considered due particularly to the 1939 and previous bushfires, declining cattle intensity and possibly to a slightly wetter climate in the years prior to 1994 (Bruce 1996).

The combined G.I.S.-aerial photography approach presented here was a viable, alternative method for determination of vegetation change in alpine environments. The approach offered both a useful way of determining environmental change on a relatively large scale, and allowed validation of many of the regenerative processes that have been observed at the smaller scale by other researchers.

REFERENCES

- ASHTON, D. H. & WILLIAMS, R. J., 1989. Dynamics of the Subalpine Vegetation in the Victorian Region. In *The Scientific Significance of the Australian Alps*, R. Good, ed., Proceedings of the First Fenner Conference on the Environment, Canberra, September 1988. The Australian Alps National Parks Liaison Committee & Australian Academy of Science, Canberra, 143–169.
- AUSTRALIAN ALPS LIAISON COMMITTEE, 1992. *Australian Alps Education Kit*. Australian Alps Liaison Committee.

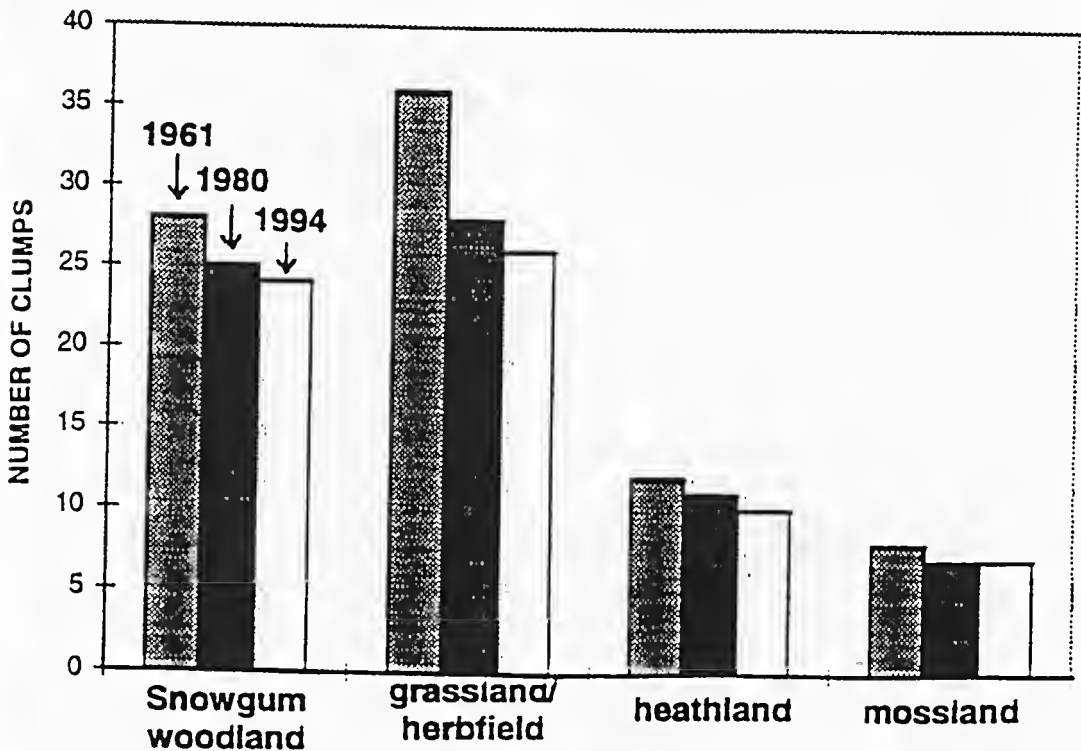


Fig. 3. Changes in the number of 'clumps' of each vegetation community in the Watchbed Creek catchment over time.

- BRUCE, C. M., 1996. *Long-term Vegetation Changes in Watchbed Creek Catchment, Bogong High Plains, Victoria*. BA(Hons) Thesis, Department of Geography, University of Adelaide.
- CABENA, P. B., 1980. *Grazing the High Country: an Historical and Political Geography of High Country Grazing in Victoria, 1835 to 1935*. MA Thesis, Department of Geography, University of Melbourne.
- CARR, S. G. M., 1977. *Report on Inspection of the Bogong High Plains 1977*. Unpublished document submitted to the Land Conservation Council, Victoria.
- CARR, S. G. M. & TURNER, J. S., 1959. The Ecology of the Bogong High Plains. 1. The Environmental Factors and the Grassland Communities. *Australian Journal of Botany* 7: 12-33.
- COSTIN, A. B., 1954. *A Study of the Ecosystems of the Monaro Region of New South Wales*. Government Printer, Sydney.
- COSTIN, A. B., 1957. *High Mountain Catchments in Victoria in Relation to Land Use*. Soil Conservation Authority, Melbourne.
- COSTIN, A. B., 1958. *The Grazing Factor and the Maintenance of Catchment Values in the Australian Alps*. CSIRO Division of Plant Industry Technical Paper No. 10.
- LAWRENCE, R. E., 1990. *The Interaction between the Environment, Land Use and Hydrology of the Bogong High Plains Area from 1850 to 1985*. PhD Thesis, Department of Geography, University of Melbourne.
- LAWRENCE, R. E., 1995. The Effects of Grazing Activity on the Hydrology of the Bogong High Plains, Australia. *Rangeland Journal* 17: 138-153.
- LAWRENCE, R. E., 1998. Vegetation Changes on the Bogong High Plains from the 1850s to 1950s. *Proceedings of the Royal Society of Victoria* 111: iii-iii.
- MCDUGALL, K., 1982. *The Alpine Vegetation of the Bogong High Plains*. Ministry for Conservation, Environment Studies Publication No. 357. Ministry for Conservation, Melbourne.
- MCDUGALL, K., 1989. *The Effect of Excluding Cattle from a Mossbed on the Bogong High Plains, Victoria*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 95.
- ROWE, R. K., 1972. *A Study of the Land in the Catchment of the Kiewa River*. Soil Conservation Authority, Melbourne.
- VAN REES, H., PAPST, W. & MCDUGALL, K., 1984. *Monitoring of the Grassland Community on the Bogong High Plains*. Soil Conservation Authority, Melbourne.
- VICTORIA, DEPARTMENT OF CONSERVATION & ENVIRONMENT, 1992. *Alpine National Park Bogong Unit Management Plan*. Department of Conservation & Environment, Melbourne.
- WAHREN, C.-H. A., PAPST, W. A. & WILLIAMS, R. J., 1994. Long-term Vegetation Change in Relation to Cattle Grazing in Subalpine Grassland and Heathland on the Bogong High Plains: an Analysis of Vegetation Records from 1945 to 1994. *Australian Journal of Botany* 42: 707-639.
- WILLIAMS, R. J., 1991. Cattle Grazing within Subalpine Heathland and Grassland Communities on the Bogong High Plains: Disturbance, Regeneration and the Shrub-grass Balance. In *Australian Ecosystems. Symposium Proceedings, Geraldton, Western Australia, 1988*, C. A. Saunders, ed., Surrey Beatty, 255-265.
- WILLIAMS, R. J. & ASHTON, D. H., 1987. The Composition, Structure and Distribution of Heathland and Grassland Communities in the Subalpine Tract of the Bogong High Plains, Victoria. *Australian Journal of Ecology* 12: 57-71.

VEGETATION CHANGES ON THE BOGONG HIGH PLAINS FROM THE 1850s TO 1950s

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Vegetation changes on the Bogong High Plains during the first century of European occupation are investigated using environmental history methodologies. Of the many land uses that have impacted the area, grazing activities have played a major role in vegetation alteration, and the historical and geographical impacts of grazing by stock on the environment are detailed. Multiple fires burned the Bogong High Plains area between the 1850s and 1950s and the distribution of affected areas is presented. The impacts of land use activities and fire on snow gum woodlands, heathlands, grasslands and mosslands are discussed and a temporal model relating anthropogenic and vegetation factors is presented.

THE environment of the Australian Alps has been changing ever since its formation (Ollier & Wyborn 1989). Geological and climatic changes have occurred over long time periods and have produced a distinctive alpine and subalpine vegetation cover in the Australian alpine area (Mosley 1988; Kershaw & Strickland 1989). This environment remains dynamic today and continues to change in response to natural forces such as climate (Williams 1990), fire (Kirkpatrick & Dickinson 1984; Leigh et al. 1987) and plague damage (Carr & Turner 1959). The arrival of people to the alps, particularly the European settlers, has initiated even more changes (Australian Academy of Science 1957; Costin 1957; Johnson 1974; Slattery 1998). For example, for the Bogong High Plains section of the Australian Alps (Fig. 1), Lawrence (1994) has outlined changes in land uses, environment and hydrology since European occupation and Wahren et al. (1994) have detailed changes in vegetation plots since their establishment in the mid 1940s. This paper compliments the work of Wahren et al. (1994) by providing detail on vegetation changes on the Bogong High Plains between the 1850s and 1950s. Environmental history methodologies have been employed for this task.

During the 1980s, the fields of environmental change and environmental history emerged as new, integrative and rapidly growing fields of study. This emergence was reflected in the explosion in major works addressing global environmental change (Worster 1988; Simmons 1989, 1993; Roberts 1989, 1994; Mannion 1991; Bell & Walker 1992; Goudie 1992; Mackenzie & Mackenzie 1995; Goudie & Viles 1997). This trend has had a counterpoint in texts examining environmental change in Australia (Bolton 1992; Dodson 1992;

Dovers 1994; Kirkpatrick 1994; Aplin et al. 1995; Young 1996). The unifying theme of these works is that all environments are dynamic and respond to the interplay of climatic and anthropogenic forces. Dovers (1994: 4) wrote:

Environmental history is the investigation and description of previous states of the biophysical environment, and the study of the history of human impacts on and relationships with the non-human setting. Environmental history seeks to explain the landscape and issues of today and their evolving and dynamic nature, and from this to elucidate the problems and opportunities of tomorrow.

The relevance of environmental history is that it aims 'to examine the past as it relates to environmental and resource issues in the present' (Dovers 1994: 6). In this way, the outcomes of environmental history are similar to palaeo-environmental studies which 'help understand the trajectory that a particular environmental system is following, and hence aid in its management' (Roberts 1989: 187).

There are many methodologies used in environmental history. Indeed, Dovers (1994: 12) claimed 'environmental history is an eclectic enterprise' and cited works in the field utilising primary and secondary sources, scientific analyses, oral histories, observation, hypothesis and speculation. Roberts (1989) provided a useful summary of modes of study that address mechanisms of environmental change over different time scales. He claimed that the traditional fields of scientific inquiry that rely on observation and experiment are applicable to environmental changes associated with ecological succession, secular climatic variation and human activities over time periods of hours, days, months and sometimes years.

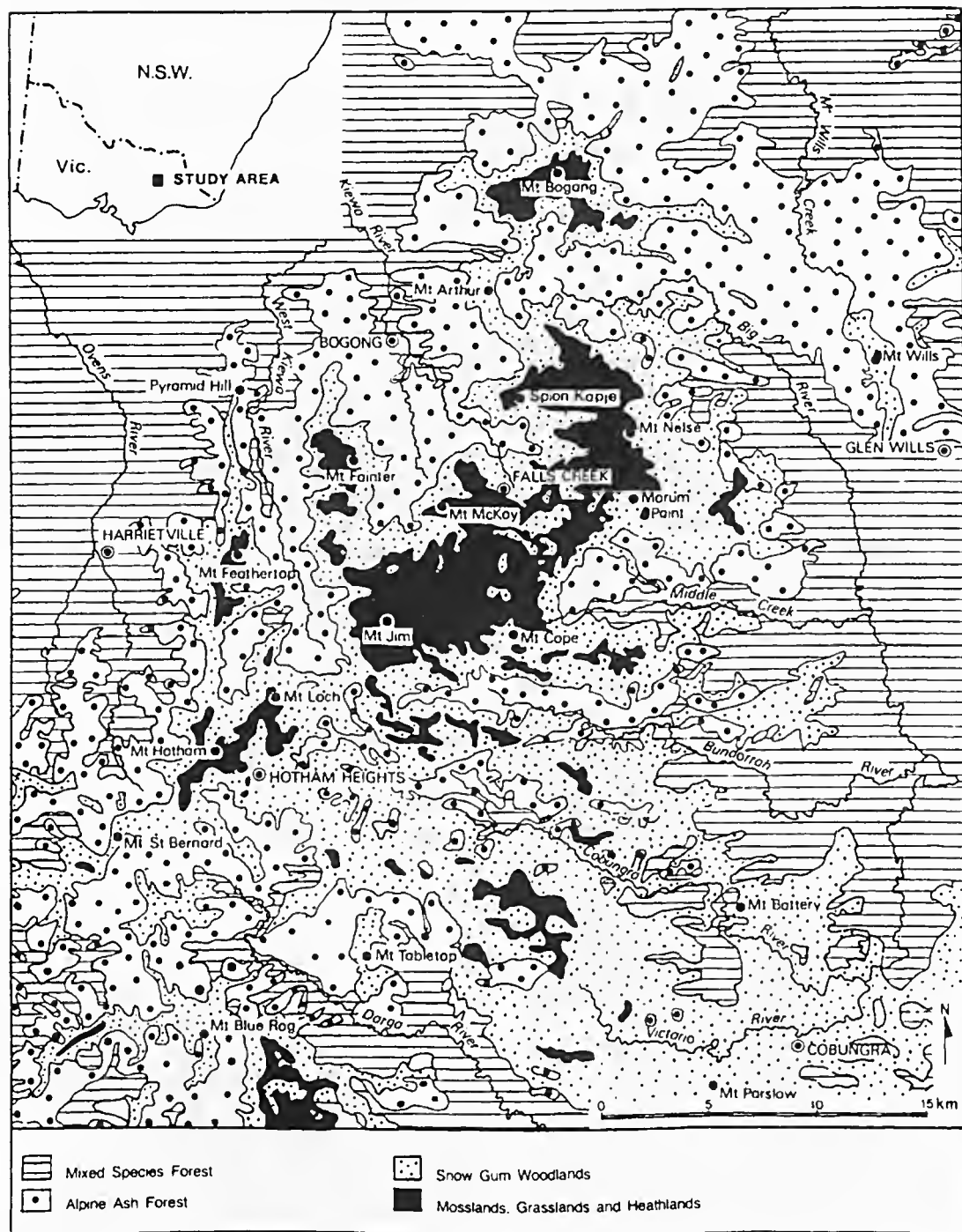


Fig. 1. Location and vegetation of the Bogong High Plains area. The vegetation communities considered in this paper are the snow gum woodlands, heathlands, grasslands and mosslands.

However, many environmental changes occur for longer time periods and so the study of those changes needs to be supplemented by additional study methodologies. Roberts (1989) suggested that documentary records and/or palaeoecological reconstruction were appropriate modes of study for processes and activities occurring over time periods of months, years, decades, centuries and millennia.

Six fields of evidence have been used to establish the vegetation history of the Bogong High Plains

area between the 1850s and 1950s. The time scale under consideration lends itself primarily to the analysis of historical documentation and has been supplemented by scientific analyses after the mid 1940s. The remoteness of the area prior to the 1940s dictated that relatively few visitors reported on the area, but those who both visited and reported on their trip have been summarised in Table 1, where at least 27 visits to the Bogong High Plains area between the 1850s and 1950s are detailed.

Year	Visitor	Purpose of visit	Areas visited
1854	Ferdinand Mueller	Botanical exploration	Mts Hotham and Feathertop areas
1869	George Neumayer	Magnetic survey	Mts Hotham and Feathertop areas
1877	Reginald Murray	Geological survey	Bogong and Dargo High Plains
1877	Alfred Howitt	Geological survey	Bogong and Dargo High Plains
1886	Robert Lendenfeld	Geological survey	Mt Bogong area
1886	James Stirling	Geological survey	Mt Bogong area
1887	James Stirling	Naturalist observations	Mt Hotham area
1888	Anonymous	Journalist writings	Bogong High Plains
1890	James Stirling	Field trip for 'Congress of Australasian Scientists'	Mt Feathertop, Bogong High Plains and Mt Hotham areas
1899	Charles Walter	FNCV trip	Mt Hotham area
1900	J. H. Maiden	Field trip for AAAS	Mt Hotham area
1904	George Coghill	FNCV trip	Mt Bogong area
1910	S. Callanan	Lands Department survey of grazing leases	Bogong High Plains
1910s	Alfred Tadgell	FNCV trip	Mt Hotham area
1920	D. Best	FNCV trip	Mt St Bernard
1922	Alfred Tadgell	FNCV trip	Mt Hotham area
1923	H. B. Williamson	FNCV trip	Rocky Valley, Pretty Valley and Bogong High Plains
1924	Alfred Tadgell	FNCV trip	Mt Bogong area
1926	Alfred Tadgell	FNCV trip	Mt Fainter and Bogong High Plains
1928	H. B. Williamson	FNCV trip	Cobungra area
1920s and 1930s	L. T. Guy and SEC personnel	SEC survey of area's hydroelectric potential	Bogong High Plains
1930	Alfred Tadgell	FNCV trip	Pretty Valley
1935	Strom & Thompson	SR&WSC survey	Mt Hotham area
1943	SEC personnel	SEC report	Bogong High Plains, Kiewa area
1943	SCB personnel	SCB survey of erosion	Bogong High Plains
1946	Turner & Fawcett	Melbourne University Botany research	Pretty and Rocky Valley plots
1947	SCB personnel	SCB Advisory Committee	Pretty and Rocky Valley plots
1948	Turner & Fawcett	Melbourne University Botany research	Bogong High Plains
1949	SCB personnel	SCB Advisory Committee	Pretty and Rocky Valley plots
1952	Reuben Patton	FNCV report	Bogong High Plains
1957	Alec Costin	SCA report	Bogong High Plains
1959	Costin, Wimbush, Kerr & Gay	CSIRO report	Bogong High Plains

Table 1. Visitors to the Bogong High Plains area, 1850s to 1950s. AAAS, Australasian Association for the Advancement of Science; CSIRO, Commonwealth Scientific & Industrial Research Organisation; FNCV, Field Naturalists Club of Victoria; SCB/SCA, Soil Conservation Board/Soil Conservation Authority; SEC, State Electricity Commission; SR&WSC, State Rivers & Water Supply Commission.

Three of the six information sources utilised were written records on the environment of the Bogong High Plains. These included published and unpublished government reports, journalist and naturalist writings, and reminiscences of residents of the area. The early reports were usually descriptive in nature and, although not always conducted with the same objectives in mind, described the alpine and subalpine environments in some detail. Most environmental reports on the Bogong High Plains between the 1850s and 1880s were made by government botanists (Mueller 1855), surveyors (Neumayer 1869), geologists (Howitt 1877; Murray 1878; Lendenfeld 1886; Stirling 1886) and land managers (Stirling 1887). Later government visits focused on the land degradation of the Bogong High Plains and resulted in reports that were both unpublished (Callanan 1910; Strom & Thompson 1935) and published (Victoria, State Electricity Commission 1935; Victoria, Soil Conservation Board 1945, 1947, 1949; Costin 1957; Costin et al. 1959). Between the 1880s and 1900s, the Bogong High Plains were visited by journalists (*Illustrated Australian News* 1888) and science organisations (Stirling 1890; Maiden 1900). The scientific trips spawned a great naturalist interest in the area over the next three decades, particularly by the Field Naturalists Club of Victoria, and their trip reports provide many insights into the environment of the Bogong High Plains between the 1890s and 1930s (Walter 1899; Coghill 1904; Best 1920; Tadgell 1922, 1924, 1926, 1930; Williamson 1923, 1929). Further information was obtained from the reminiscences of those who resided near, and frequently visited, the alpine and subalpine area. These proved to be particularly useful in reconstructing the fire history of the Bogong High Plains area (Rush 1939; *Schluss* 1939; Weston 1939; Fawcett 1955; Holth 1980; Edmondson 1984).

Period maps and photographs were the fourth and fifth fields of evidence used to establish the vegetation history of the Bogong High Plains. Many of the reports mentioned above were accompanied by maps and photographs and they were supplemented by other cartographic and photographic collections held in such places as the State Library of Victoria. Period maps gave a spatial dimension to the general nature of the written record and were particularly useful where annotations were provided. Of notable use for this project were vegetation and fire history maps held by government department offices local to the Bogong High Plains area. Archival photographs provided an unrivalled source of supplementary data to the written record particularly when the

date and location of the photograph were known. The acquisition of over 100 sketches and photographs of the Bogong High Plains taken between the 1850s and 1950s allowed for the analysis of vegetation changes in a manner not possible from written records alone. Sequential photography was particularly useful in this regard. For example, photographs looking towards Mt Feathertop from the Mt Hotham area (Fig. 1) were obtained for 1888, 1900, 1911, 1922, 1934 and 1958, providing a comprehensive record of the history of vegetation cover in that area.

The final source of information used to establish the vegetation history of the Bogong High Plains during the first century of European occupation was scientific analyses. The ecological studies conducted by the University of Melbourne School of Botany in association with the Soil Conservation Authority (and subsequent government authorities) provided quantitative data on the ecological nature of the Bogong High Plains after the mid 1940s (Turner & Fawcett 1946, 1948; Paton 1953; Carr & Turner 1959; Wahren et al. 1994). This was the first scientific investigation into the role of disturbing agents such as cattle grazing and fire on the composition and cover of the vegetation of the Bogong High Plains. Unpublished dendrochronological work conducted on subalpine vegetation communities in the Bogong High Plains area has also been utilised in this study.

Using the methodology and sources of information outlined, changes in the type and coverage of four broad vegetation communities of the Bogong High Plains are detailed in this paper. Of the vegetation communities shown in Fig. 1, attention is directed to the snow gum (*Eucalyptus pauciflora*) woodlands, heathlands, grasslands and mosslands of the alpine and subalpine areas. The heathlands have been classified by McDougall (1982) as dominated by either *Podocarpus*, *Phoebe*-*Bossiaea*, *Hovea*, *Grevillea*, *Kunzea* or *Epacris* and may be either closed or open in structure. The term grassland characterises vegetation communities dominated by either *Poa* species, snow patch species, *Caltha* herbs or *Celmisia* herbs (McDougall 1982). Mossland communities denote bog, fen and *Carex* sedge/land species that typically occupy the broad valley floors of the area.

The dominant cause of vegetation change on the Bogong High Plains between the 1850s and 1950s has not been climatic variation, although such has occurred (Lawrence 1998a), but rather land use activities and fire. Thus, before examining the vegetation history of the snow gum woodlands, heathlands, grasslands and mosslands of the Bogong

High Plains, an overview of the land use and fire history of the area is provided.

LAND USES PROMOTING VEGETATION CHANGE

Aboriginal people regularly visited the Australian alpine area between the end of the last glacial period and the 1850s to feast on the Bogong moth (*Agrotis infusa*). Flood (1980: 62) claimed:

[The] Aborigines had little or no effect on high altitude vegetation, for they would have spent only a few weeks on the mountain tops each summer, would have utilised naturally open frost hollows and ridge tops as routes, and would have had no need of widespread fires for hunting Bogong moths, or for the hunting of game, since terrestrial mammals are few at these high elevations.

It appears that the establishment of multiple pathways through the alps and the use of small campsites for cooking were the only environmental legacies of the Aborigines in the Australian Alps. No evidence has been found to support the notion that the Aborigines regularly burned alpine and subalpine vegetation communities and, in fact, there is anecdotal evidence to the contrary (Fawcett 1955). Under these land use practices, it is surmised that the alpine and subalpine vegetation had reached and maintained climax conditions where grassland communities predominated over shrublands (Lee 1979) and mosslands maintained a high water content in the valley floor areas.

Since the 1850s, the environment of the Bogong High Plains has been subject to changes due to climatic and anthropogenic factors (Lawrence 1994). In 1895, there was a reduction in the annual precipitation over much of Australia including the Bogong High Plains area (Deacon 1953). A second change occurred in 1945 when the annual precipitation over southeastern Australia increased (Pittoek 1975). Lawrence (1998a) has demonstrated that seasonal precipitation increased by as much as 20% after 1945 in the Bogong High Plains area and argued that those climatic changes were the driving force for land use changes in the area, especially changes in the grazing and fire regimes. The most prolonged and contentious land use in the Bogong High Plains area has been grazing by introduced stock during the summer months each year. Both grazing and fire affect the vegetation extensively and a discussion of these factors follows. Other anthropogenic contributors to vegetation changes are intensive land uses such as mining, hydroelectricity production and ski

village development. The manner in which these land uses impacted on the vegetation of the Bogong High Plains will be subsequently addressed.

Chronology of grazing activities

Grazing of the alpine and subalpine vegetation by introduced stock has been a long-term feature of the European land use history of the Bogong High Plains area. Carr (1962) recorded that the Bogong High Plains were discovered by stockmen, under direction from Aborigines from the Mitta Mitta Valley, who were looking for pastures to graze their stock in the wake of the 1851 bushfires. Between 1857 and 1887, the Bogong High Plains and Mt Bogong areas were part of the 'Bogong High Plains' squatting run and after 1866 the Bogong High Plains were used as summer grazing land for sheep and cattle (Howitt 1879). Holth (1980) recorded that sheep from the Ensay station south of Omeo were sent to the Plains during a drought year in the early 1880s. This marked the first of several seasons when large numbers of stock grazed on the Plains. In 1883, graziers from the Ovens and Kiewa valleys arranged with the Ensay station owners to depasture cattle and horses on the Bogong High Plains, and during the following summer two pastoralists from the drought stricken Riverina in New South Wales did likewise (Cabena 1980). In 1884, one pastoralist brought 11 000 sheep to the area that, combined with the stock belonging to local graziers, resulted in the grazing of between 18 000 and 20 000 sheep on the Bogong High Plains and Mt Hotham area over the 1884–85 summer (Table 2). The grazing of cattle on the summit of Mt Bogong also commenced in the early 1880s (Holth 1980).

Government oversight of summer grazing activities on the Bogong High Plains commenced with the passing of the 1884 *Land Act* when squatting tenure was formerly ended. In 1887, the 'Bogong High Plains Green Area' was declared and pastoralists were granted an annually renewable grazing licence to run stock in the area (Cabena 1980). Ten years later, other graziers expressed interest in the Bogong High Plains as a summer grazing venue due to the following three factors: firstly, the general economic depression of the 1890s produced many unemployed people, some of whom looked to farming as a means of survival; secondly, the decline in mining activity led a number of miners to take out selections in the region; and thirdly, the spread of rabbits, which had begun to infest the Victorian landscape in plague proportions (Holth 1980), drastically reduced the productivity of the lowland pastures and

initiated considerable land degradation (Faweett 1955). Several graziers in northeastern Victoria looked for alternative grazing lands and 'rabbit relief' pastures were identified in the Bogong High Plains Green Area.

The grazing activities on the Bogong High Plains and surrounding peaks between the 1890s and 1920s have been outlined by Lawrence (1995) and are summarised in Table 2. Of particular note during this era was the occurrence of three severe droughts early this century that resulted in excessive numbers of stock in the high country.

Over the 1902–03, 1907–08 and 1914–15 summers, an additional 40 000 sheep, 12 000 cattle and 40 000 sheep were sent to the Bogong High Plains area respectively. These stock were grazed in addition to the regular stock sent to the area. The drought conditions in the Upper Murray and Riverina areas were also felt in the alpine region. Although the Victorian Government was responsible for the issuing of annually renewable licences in those days, they did not play an active role in land management but rather left the graziers to conduct their business as they liked (Cabena 1980).

Grazing season	Areas grazed	Numbers and types of stock grazed
1866–78	Bogong High Plains (specific grazing area not known)	Cattle and sheep
Early 1880s	Dinner Plain and Mt Jim	Sheep from Ensay station
1882	Mt Bogong summit	Cattle from the Kiewa Valley
1883	Bogong High Plains	730 cattle and 40 horses from the Kiewa and Ovens Valleys; none from Ensay
1884–85	Bogong High Plains, Mt Bogong and Mt Hotham areas	20 000 sheep from the Riverina, northern Victoria and the local area, as well as cattle
1884–1910s	Mt Bogong summit	2000 cattle every year from Eskdale
1890s	Dinner Plain and Mt Jim areas	At least 600 horses from Benambra
1890s–1914	Mt Feathertop and the Razorback Ridge	2000 cattle and about 80 horses from Germantown
1890–1923	Mt Hotham and Mt Jim areas	2000 cattle and 20 horses from Harrierville
1902–03	Bogong High Plains, Mt Bogong and Mt Hotham areas	40 000 sheep and several thousand cattle from the Riverina, northern Victoria and the local area
Early 1900s	Bogong High Plains	1000 cattle and 200 horses from Tawonga
1908	Bogong High Plains	12 000 cattle plus sheep from the Gippsland and Omeo areas
1910	Bogong High Plains	3000 cattle and 300 horses
1914–15	Bogong High Plains, Mt Bogong and Mt Hotham areas	40 000 sheep, many from NSW and northern Victoria, as well as cattle
1919	Mt Bogong summit	300 cattle from the Mitta Mitta Valley and 2000 cattle from Eskdale
1920s	Mt Bogong summit	300 horses from Tawonga and 2000 cattle from Eskdale
1920–1940	Bogong High Plains	Nearly 10 000 cattle from Omeo, the Kiewa and Ovens Valleys
1923	Bogong High Plains	6000 cattle from northeastern Victoria left on Plains for an extended period
1928	Mt Cope area	2000 sheep from Omeo
1930s and 1940s	Mt Bogong summit	2000 cattle and some horses from the Mitta Mitta Valley
1939–40	Bogong High Plains	Sheep from Omeo
1939–40	Mt Feathertop	300 sheep from the Ovens Valley
Late 1940s	Bogong High Plains, Mt Bogong, Mt Hotham and Mt Feathertop	9000 cattle from the Ovens Valley, Kiewa Valley and Omeo area
Late 1950s	Bogong High Plains	5000 cattle from the Ovens Valley, Kiewa Valley and Omeo area

Table 2. Numbers and types of stock grazed in the Bogong High Plains area for specific years between the 1850s and 1950s. *Source:* Schuss (1939); Cabena (1980); Callanan (1910); Holth (1980); Howitt (1879); Pearson (1969); Stephenson (1980); and grazing data for the late 1940s and 1950s held by Parks Victoria.

During the 1920s and 1930s there was an increase in the number of graziers from the Omco area and the Ovens and Kiewa valleys who sent stock to the Bogong High Plains area. This trend was largely due to improvements made in the lowland pastures which, combined with a brighter economic outlook, encouraged graziers to invest in larger numbers of stock, thereby necessitating an increased use of the alpine and subalpine pastures (Cabena 1980). Droughts did not feature during this period (Lawrence 1995) and about 10 000 cattle were sent to the Bogong High Plains Area from Omco and the Ovens and Kiewa valleys each summer (Table 2). However, the drought conditions of 1939 again saw large numbers of cattle in the Bogong High Plains area as well as several flocks of sheep. The 1939 bushfires swept over the Plains causing a substantial loss of vegetation that combined with the grazing densities of the 1938–39 summer ultimately led to the regulation of grazing leases in the Victorian alpine area.

In the early 1940s, the State Electricity Commission and the Soil Conservation Board expressed concern about the deterioration of the Bogong High Plains due to uncontrolled grazing activities (Lawrence 1995). In 1946, the Soil Conservation Board set up an 'Advisory Committee' consisting of government delegates and representative cattlemen, which aimed to 'determine the number of cattle which should be taken onto the Bogong High Plains each season and also the period within which the cattle may be depastured there' (Victoria, Soil Conservation Board 1946). The grazing of sheep on the Bogong High Plains was forbidden by the Committee—a move which was welcomed by the cattlemen—and the dates of entry of the cattle to the High Plains and the timing of the final muster were to be decided annually in accordance with the conditions of both the lowland and highland pastures (Mitchell 1968).

Since 1945, there has been a general decline in grazing activity in the Bogong High Plains from about 9000 cattle in the late 1940s to about 5000 in the late 1950s (there are about 2000 cattle grazing the area today). During the late 1940s some leaseholders withdrew their interest in the area as they found that the grazing of stock on the High Plains was uneconomical following the 1950 slump in cattle prices, and other graziers retired (Holth 1980). Since the mid 1940s, cattle have usually been taken onto the High Plains during December and mustered around Easter time.

The leases covering areas that suffered heavily from overgrazing were withdrawn from use following the establishment of grazing controls. In 1955, a fence was constructed on the southeastern side

of Mt Bogong to restrict the available grazing area in the Mt Bogong area to the Long Spur. In 1958, the Mounts Hotham, Loch and Feathertop areas were closed to grazing (Victoria, National Parks Service 1983) when a rough fence was erected below Mt Loch to prevent cattle wandering to the summit areas. The completion of State Electricity Commission construction works such as the Rocky Valley Reservoir during the late 1950s also rendered other grazing runs ungrazable.

Distribution of grazing activities

The distribution of livestock on the rangelands has never been uniform and has been influenced by many factors. Some sites were heavily grazed while others were avoided. The grassland areas were the most favoured places for sheep grazing as this reduced the risk of the animals being caught in the heathland vegetation that lowered the value of their wool. Horses preferred to roam the snow gum woodland and adjacent open plains areas that were not subject to excessive snow cover (Cabena 1980). Brumbies still roam the Dinner Plain and Mt Jim areas and these originated from horses grazed by the Youngs from Benambra in the 1890s. The distribution of cattle on the Bogong High Plains was researched by van Rees (1984) who found that the most important variables affecting the behaviour of cattle on the Plains included: the steepness of slope, slope angles adjacent to and near water, distance to water, floral composition of palatable plants, thickness of shrubs, location of salt, extreme weather conditions, and home range behaviour. Van Rees (1984) found that cattle generally preferred grasslands and heathlands for grazing and utilised mossbeds as their primary source of running water. Sites where graziers placed salt licks were heavily trampled because they were preferred resting areas. It was found that cattle tended to remain on the run that had been assigned to their owners and, even though some intermingling of cattle from adjacent runs did occur, that it was unusual to observe cattle a long distance from their run.

Although the factors influencing livestock distribution on the Bogong High Plains and surrounding peaks have been ascertained by van Rees and others, no analysis of the grazing densities in the area has yet been made. One reason for this lack is that the number of cattle per square kilometre of grazing run is not meaningful, as not all areas of each run are grazed evenly. However, when a number of assumptions based on van Rees (1984) work are made, meaningful grazing density maps

can be developed. 'Effective grazing areas' are defined as the maximum part of the Bogong High Plains area subject to the variables identified by

van Rees (1984), and stock numbers per effective grazing area are mapped for the 1949-50 summer in Fig. 2.

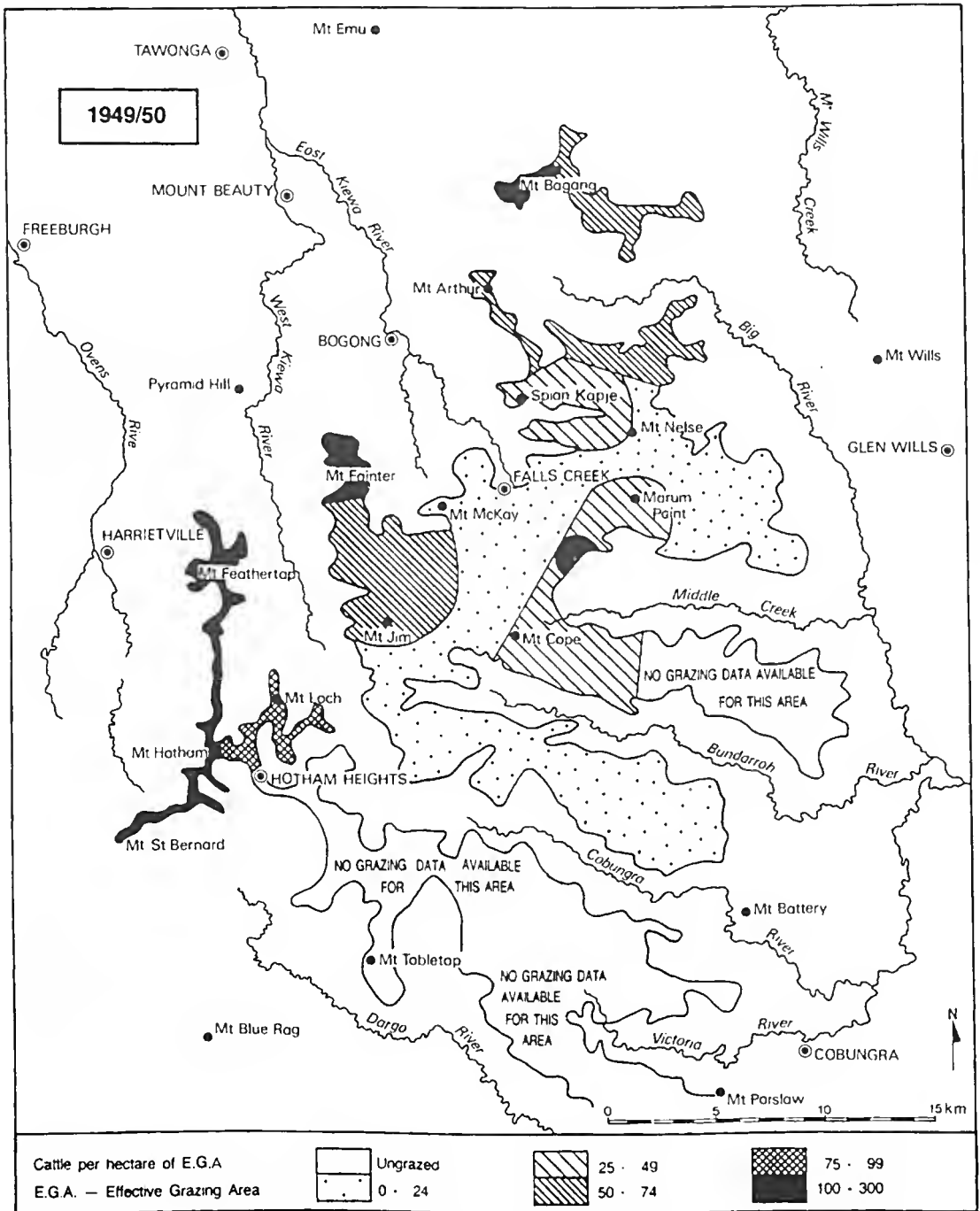


Fig. 2. Grazing densities in 'effective grazing areas' on the Bogong High Plains during the 1949-50 summer.

From the analyses of grazing densities per effective grazing area, a couple of interesting observations are made. Firstly, the isolated areas of alpine rangeland in the Mounts Feathertop, Hotham, Loch and Bogong areas were all heavily grazed in 1949–50. It was undoubtedly those high stocking rates that contributed to the historical evidence of erosion (Lawrence 1994), and the subsequent decision of the Advisory Committee to restrict grazing from these areas. Secondly, it is apparent that the western edge of the Plains between Mounts Fainter and Jim, the Mt Nelse region, and the area between Marum Point and Mt Cope were subjected to high grazing densities between the mid 1940s and mid 1980s (Fig. 2). However, unlike the isolated grazing areas, there was no physical obstruction to prevent stock from straying to other parts of the High Plains, so this finding is only of moderate significance.

The post-1945 cattle numbers should be compared to the numbers given in Table 2 when stock numbers sometimes achieved the six-digit mark. By way of comparison, if a map equivalent to Fig. 2 was drawn for either the 1902–03 or 1914–15 summers the whole area would be heavily shaded, as the average densities would be over 170 head of stock per square kilometre of effective grazing area. This points to the fact that grazing by stock has decreased dramatically since the drought years early this century, and is a trend that has continued since the introduction of grazing controls in 1945.

Intensive land uses

At the same time that grazing activities were extensively impacting on the vegetation of the Bogong High Plains, several intensive land uses were affecting local areas. Mining for gold occurred mainly in the large valleys surrounding the Bogong High Plains and gave rise to the establishment of the towns of Harrierville, Cobungra and Glen Wills (Fig. 1). Several auriferous reefs were discovered and worked in the Mt Hotham area and along the Razorback, and alluvial and deep lead deposits were mined near Mt Fainter and in the headwaters of the Cobungra and Dargo rivers. Exploration for gold also took place on the southern slopes of Mt Bogong. Most gold mining activity occurred between the 1850s and 1890s, and the 1880s was the era when a concerted effort was made on the part of the Victorian Government to locate gold deposits in the mountainous country including the Bogong High Plains. There was a minor resurgence

of interest in the 1940s and 1950s when the Red Robin reef was discovered near Mt Hotham (Lawrence 1998b).

The impact of gold mining activities on the alpine and subalpine vegetation commenced with the exploration of the area. The miners typically burnt the country to locate the ore and this practice is discussed in the next section. Once the ore body was located, a network of tracks and accommodation venues were established. In the Bogong High Plains area, some of the tracks were accompanied by snow pole lines to ensure safe passage for the miners in inclement weather. At the site of the ore body, plant cover was dislocated. In the case of reef gold, the vegetation was either trampled or covered by mullock heaps. Where the gold was contained in deep leads and buried by overburden such as basalt, racelines were constructed to provide the water necessary for sluicing. This gold mining method was particularly destructive to the environment as large amounts of rock and soil were relocated from above the ore deposit to the downslope side of the mine site and the fine particles found their way into the river systems. All vegetation in the vicinity of the mines was invariably destroyed and the scars that remain at mining sites near Mt Hotham today (over a century later) are testimony to those severe impacts. Valley vegetation communities were particularly vulnerable to disturbance in one of the following ways. If the stream was truncated by a raceline, the downslope sector was subject to water depletion. By contrast, if the stream received run-off from the mine site it would have been subject to sediment overload. It is thought that mossbeds downstream of the Mounts Hotham and Fainter workings would have been so clogged with sediment as to render them ineffective.

The Kiewa Hydro-Electric Scheme was constructed to utilise the waters of the Upper Kiewa River between the late 1930s and the early 1960s. The main alpine and subalpine areas disturbed were located in the headwaters of the Pretty Valley and Rocky Valley streams. In those areas, about 100 kilometres of roads and tracks were constructed, two major and five minor work sites and accommodation centres were established, the Rocky Valley Reservoir was built, the Pretty Valley Reservoir was commenced but later abandoned, about 35 kilometres of aqueducts were constructed, and one major and several minor quarries were excavated. As was the case for mining, those areas where construction activities took place were subjected to extreme vegetation disturbance, especially the valley environments downstream of the construction sites and aqueducts.

Vehicular trampling and excavation activities were particularly problematic as the destruction of vegetation communities by these activities was indiscriminate.

The third intensive land use in the Bogong High Plains area was the development of the ski villages of Falls Creek and Mt Hotham. Development of those villages commenced immediately following World War II and has been continuing ever since. During the time period under consideration, the main facets of development were the construction of ski lodges and primitive rope tows at the two resorts. This entailed vegetation disturbance in the immediate vicinity of both the buildings and rope tow structures and the associated relocation of eroded material to the streams. The early developments at the two resorts would have seen the clearance of selected snow gums and shrublands as most of the construction took place on relatively flat land away from the streams.

THE INCIDENCE AND DISTRIBUTION OF FIRE

As well as the extensive land use of grazing and the intensive land uses of mining, hydroelectric scheme construction and ski village development, the other major factor influencing vegetation change on the Bogong High Plains was fire. This section addresses the characteristics, causes and geographic extent of fires in the Bogong High Plains area.

Characteristics and causes of fire

Fire has long been an important feature of Australia and many Australian plant species are adapted to fire (Commonwealth of Australia 1996). Most of the vegetation communities of the Bogong High Plains area have developed adaptive mechanisms that have enabled them to survive dramatic environmental events such as fire (Good 1992). For example, after a snow gum is burnt, it usually sprouts new growth from its lignotuber (an underground swelling containing food material capable of producing new shoots). Many of the subalpine and alpine species are adapted to fire and the recovery intervals of vegetation in the Bogong High Plains area to fire have been estimated by the Victorian Interim Reference Advisory Committee (1977).

The causes of fire in the Bogong High Plains area include natural phenomena and deliberate, inadvertent or negligent acts by people (Victoria, Department of Conservation and Environment 1992). The most common causes of fire in the

alpine and subalpine areas are lightning strikes associated with thunderstorms during the summer months. Fires originating from this cause often burn themselves out or are suppressed by fire-fighting crews. Fires that are intentionally lit as part of a management programme are variously known as either 'control burns', 'prescribed burns', 'regeneration burns' or 'fuel reduction burns'. Edgell (1973) claimed that there is a strong link between bushfires and controlled burning, and stated that bushfires are predominantly a human induced hazard but in their subsequent behaviour—unpredictability, uncontrollability and energy release—they act as natural hazards.

The use of fire by Aborigines in the alpine and subalpine area has long been debated. There is no doubt that some Aboriginal groups in Australia practiced 'fire-stick farming' in the course of hunting, to regenerate plant food for both people and their prey, and for many other purposes (Kohen 1995). This practice was recorded by Hume and Hovell in the Murray Valley near Albury in 1824 (Andrews 1981). Fawcett (1955) examined the question of traditional burning by the Aborigines of the Omeo region and gave evidence that 'fires were lit for the purpose of obtaining small game' but that 'the area burnt at any one time was limited to one or two acres [less than one hectare]'. Furthermore, the Aborigines of the Omeo area 'showed skill and judgement in the management of the fires and took great care not to let them get out of hand' (Fawcett 1955). As stated earlier, Flood (1980) presented evidence that only the lowland areas adjacent to the high country were fired.

Miners and prospectors were probably the first to utilise fire in the Bogong High Plains area. Fawcett (1955) wrote that 'the long grass which covered the country in those days was a nuisance to the miner looking for outcropping reefs or trying to locate them by "loaming"' and that 'fire was a simple way of removing the dense ground cover and it was used extensively'. Smart (1883) recorded that prospectors in the Harrierville area, who were impeded by dense vegetation, expected the summer fires to solve their problems, and Stirling (1886) reported burning by miners in the Big River Valley in 1885. Edmondson (1984) recalled fires that occurred in the Harrierville area 'about every three years' and 'which crept about for weeks' during the 1870s and 1880s. The Aborigines protested against the fires on account of their hunting grounds being destroyed, and the graziers also disapproved of the practice and attempted to extinguish those that affected them personally (Fawcett 1955).

Burning by high country graziers was not extensive during the 19th Century, but the combination of the financial crash of the 1890s, the spread of the rabbit, and the drought of 1901 reduced many settlers to poverty. An exploitative attitude then followed and the use of Crown lands as a cheap source of grass began (Faweett 1955: 89):

When times became difficult for the graziers they were armed with the knowledge [from the miners] that burning the bush forced it to produce a lush growth of grass and took advantage of it ... Graziers' practices in burning the bush have varied greatly ... and ranged from no burning at all, to lighting the bush wherever and whenever possible. Those men holding high class country as runs did not, in general, favour burning it, but those with poorer land burnt theirs very thoroughly in an attempt to make it keep on producing grass. Thus some of the run holders on the high basalt country in the Cobungra area did not burn the bush and it has never been the cattlemen's policy to burn the Bogong High Plains ... But over the greater part of the Crown lands fire has been used widely as a means of improving the herbage available for stock.

The practice of burning by graziers became widespread during the first half of the 20th Century, and three-quarters of the 1914 bushfires in Victoria were attributed to fires lit by graziers (*The Age* 1914). The unrestricted lighting of fires on Crown lands for mining or grazing purposes was prohibited in 1926 (Victorian Government 1926). This regulation was met with a mixed response on the part of the graziers. Some cattlemen continued to burn their forested runs around the Bogong High Plains until the 1970s, while others ceased the practice and watched the grazing value of the vegetation cover decline. The current feeling among the grazing community is that the restrictions have caused the fire risks now prevalent in the Alps (Commins 1995). This belief is widespread (Holth 1980), but it is probably not well founded as Faweett (1955) pointed out that the 1939 fires swept unchecked through the forests surrounding the Bogong High Plains despite regular and systematic burning in some areas prior to that date.

Geographic extent of bushfires

There have been countless fires that have burned in the Bogong High Plains area. Some fires have only burnt small areas, whilst others have burnt the forest understorey to the exclusion of the crown vegetation, and the distribution of these fires has gone largely unrecorded. Following is an outline

of the major bushfires that have impacted the Bogong High Plains area as determined from the multiple historical sources outlined earlier.

In January 1851, a large part of Victoria was burnt and 'a total darkness overspread the whole of Gippsland, and literally changed day into night' (Finn 1888). Turner (1904: 333) claimed that the only portion of the state not affected by this fire was 'the interior of Gippsland' or the Victorian high country. Faweett (1955) presented evidence that the area around Omeo was not affected by the 1851 fires, and the Cobungra area and the Bogong High Plains were evidently not burnt as feed for stock was found in those areas immediately following the fires (Carr 1962). It is probable that Lendenfeld's (1886) reference to the large number of fallen trees that made progress along the Eskdale Spur difficult in 1886 indicated a forest or woodland stand that had been burnt in 1851.

Over the next 50 years a number of fires occurred in the Bogong High Plains area (Fig. 3). Mueller reported one that impeded his botanical explorations in 1854, which is assumed to have occurred east of Mt Wills. Bushfires resulting from unchecked miners' fires occurred frequently around Harriettville during the 1870s and 1880s (Edmondson 1984) and photographic evidence indicates that some of the miners' fires crept over the Razorback into the West Kiewa Valley. The first fire in the Cobungra area was documented by Faweett (1955) to have occurred during the late 1870s: the stock responded to the burnt area so enthusiastically that the locals made special trips to observe the phenomenon.

Part of the Upper East Kiewa Valley was burnt in 1901. Edmondson (1984: 46) claimed that 'it appeared to be the first bad fire in that area and it burned for about two months'. The affected areas included 'all the snow gum on the northern approach to the Alps and Bogong High Plains', two patches of forest on the western fall of the Bogong High Plains between Mounts Fainter and Jim, and the Diamantina River area. Another fire occurred in the vicinity of the Bogong High Plains in 1914 (Edmondson 1984) and two huts on the Fainter Spur were burnt that season. Dendrochronological analyses of the forests in the Middle Creek area suggested that a fire occurred in that area in 1919 (Hardy 1956). In 1923, the lower Kiewa Valley and the foothills above Tawonga were burnt, and the bushfire was witnessed to approach Mt Bogong from the south but it did not reach the summit area (Tadgell 1924).

Between 29 January and 11 March 1926, 426 fires were reported in Victoria (Foley 1947). Tadgell (1926) witnessed a fire that burnt both sides of

the Razorbaek, the Niggerheads, and the Fainter Spur in February 1926. Strom & Thompson (1936) visited the area ten years later and reported on the

condition of the alpine region with supplementary photographs, and Edmondson (1984) provided another account of the areas burnt. These reports,

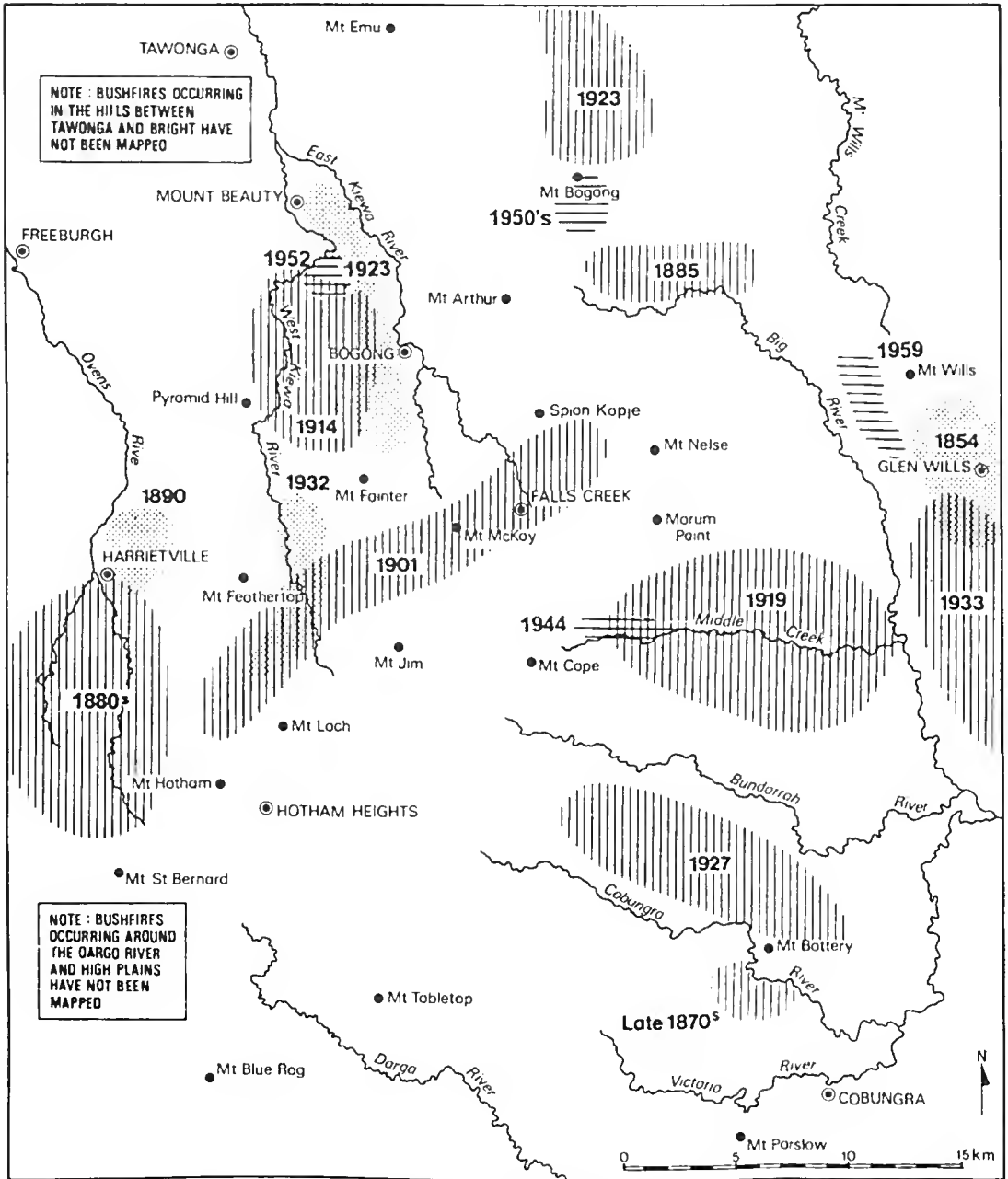


Fig. 3. The distribution of fires in the Bogong High Plains area between the 1850s and 1950s, excluding 1926 and 1939. Note that many fires during the later decades of the 19th Century have gone unrecorded.

along with contemporary photographs, have provided a comprehensive coverage of the areas affected, and the extent of the 1926 bushfires in the Bogong High Plains area is shown in Fig. 4.

The unusual phenomenon of the burning of mosslands was first reported during the 1926 fires when Edmondson (1984) recalled that the basalt plain north of Mt Jim was badly burnt and smouldered

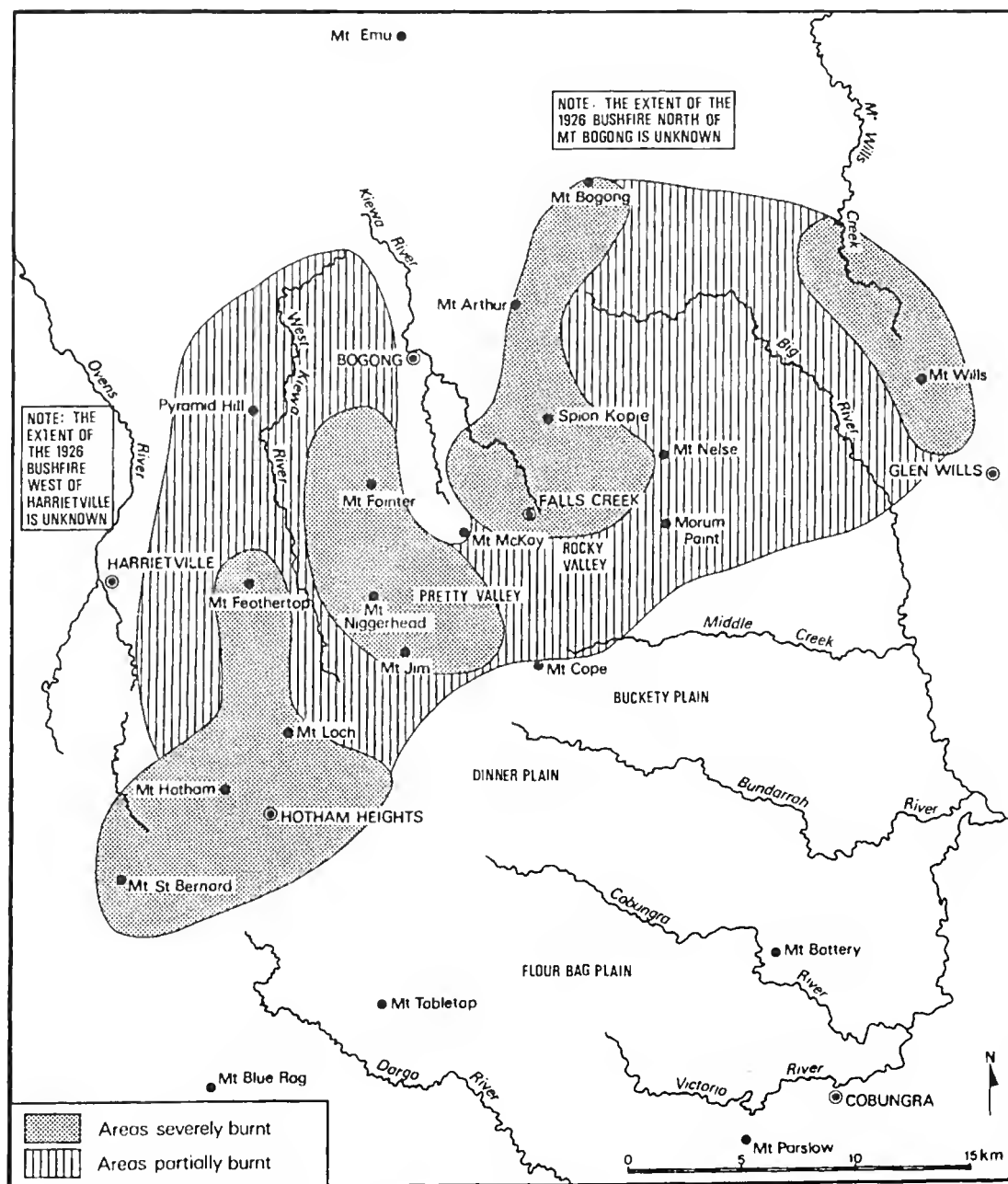


Fig. 4. Areas of the Bogong High Plains area burnt during 1926.

indefinitely. *Sphagnum* mossbeds are characterised by their high water to organic content ratio and as such are rarely subjected to fire.

The Bundarra and Cobungra River areas, which apparently escaped the 1926 fires, were burnt the following year (Holth & Holth 1985). In January 1932 a fire burnt in the 'hills higher up the Kiewa Valley' (Foley 1947), and ring counts in several patches of forest in the West Kiewa Valley date from that fire. The Big River Valley east of the Bogong High Plains was burnt in 1933 (Fig. 3).

The 1939 fires eclipsed all the previous fires by damage to property, flora and fauna in Victoria. Stretton (1939: 5) recorded that:

Numerous fires which ... had been burning separately ... either 'under control' as it is falsely and dangerously called, or entirely unattended, reached the climax of their intensity and joined forces in a devastating confluence of flame on Friday, the 13th of January.

The fire front that burnt the Bogong High Plains began as a number of independent burns in the lower Kiewa Valley, the Ovens Valley and elsewhere (Noble 1977). On 13 January 1939, the Ovens Valley fires united and advanced south-easterly towards Harrierville and Mt Hotham causing 'extreme devastation in a narrow strip about fifteen miles [24 kilometres] wide which took in the townships of Omeo and Cobungra' (Fawcett 1955). Within five hours of its passage through Harrierville every homestead and hut between the Upper Ovens Valley and Omeo was destroyed (Pearson 1969). The northern slopes of the Bogong High Plains (the Rocky Valley and Pretty Valley areas) were largely denuded when a backburn that had been started by the State Electricity Commission escaped out of control. Mossbeds at the head of McKay Creek and near Mt Jim burnt for four months after those fires (Edmondson 1984). Yet, despite the devastation of large areas of alpine and subalpine vegetation, no stock were removed from the Bogong High Plains in 1939, indicating that there was still some feed available following the fires. Fig. 5 depicts the geographic extent of areas burnt in 1939 and indicates that 75% of the Bogong High Plains area was affected by those fires.

Before the last of the 1939 fires had been extinguished, a Royal Commission was appointed by the Victorian Government to enquire into the causes and origins of the bushfires and to suggest measures necessary to prevent their recurrence (Stretton 1939). This resulted in the establishment of the Country Fire Authority in 1945 and there has never been a repeat of the 1939 experience.

Even the Ash Wednesday fires of February 1983 only burnt 28% of the area devastated in 1939 (Victoria, Forests Commission 1983). During the 1940s and 1950s, only three small fires burnt parts of the Bogong High Plains area: in 1944, 1952 and 1959 (Fig. 3). Today, most snow gum stands on the Bogong High Plains date from the 1926 and 1939 fires, and the dense growth of shrubs is a legacy of bushfires and controlled burns conducted by prospectors, graziers and Government agencies.

VEGETATION CHANGES

This section details changes to the vegetation of the area evident from the sources outlined at the start of this paper. Most written descriptions of the alpine and subalpine vegetation were found to be general comments and broad scale impressions of the area. Detail on specific changes was usually provided by the examination of period photographs. Although the Bogong High Plains area has been subject to isolated intensive and severe land uses, the following descriptions relate mostly to the extensive nature of the vegetation cover between the 1850s and 1950s.

Snow gum woodlands

Snow gum woodlands occur in pure stands between about 1400 and 1600 metres elevation, and in isolated pockets on some of the ridges and peaks of the alpine plateaux. The pure stands were first described in 1886 by Lendenfeld who recorded that dense stands of snow gums covered the Eskdale Spur north of Mt Bogong. He referred to the many 'fallen trees, the stems of which seem to resist decay for a long time' (Lendenfeld 1886). The island stands of snow gums were noticed by Murray (1878) when he described the Bogong High Plains as consisting of 'undulating plains ... interspersed with clumps and belts of snow gums'. An anonymous writer also referred to isolated patches of 'snow scrub' (*Illustrated Australian News* 1888), and many other visitors to the area referred to the snow gum woodlands of the plateaux areas (Callanan 1910; Tadgell 1926; Guy 1935). The distribution of snow gums in this fashion has been shown to be a natural phenomenon that is not related to the modification of the subalpine area by Aborigines or Europeans (Slayter 1989). McDougall (1982) stated that the presence of snow gums in clumps or islands on the plateaux areas was regulated by patterns of cold air

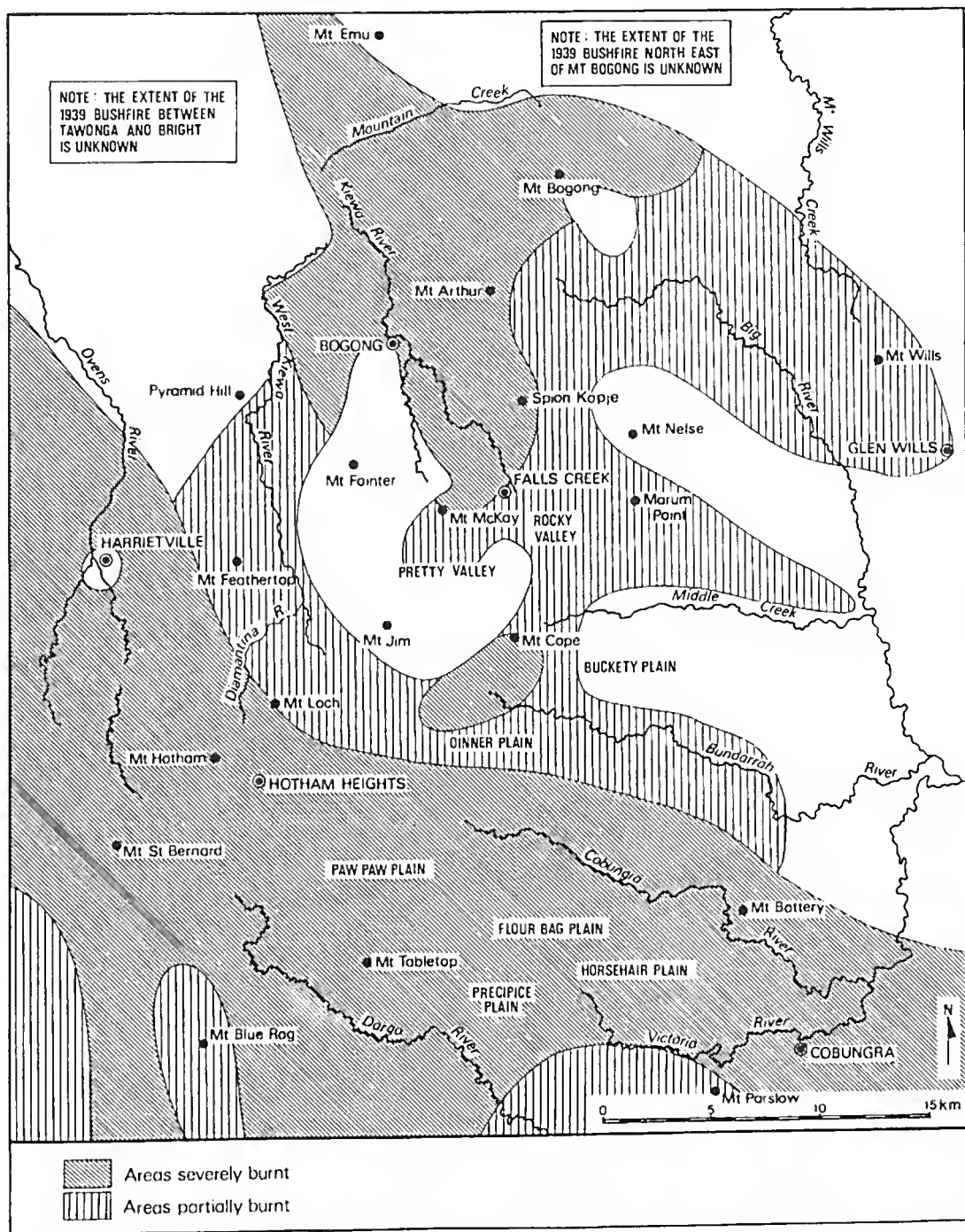


Fig. 5. Areas of the Bogong High Plains area burnt during 1939.

accumulation, while Ashton & Williams (1989) found that individual snow gums which had established themselves in a cold air drainage zone were permanently maintained in a juvenile state due to damaging frosts. It does not appear that the geographical distribution of snow gum woodlands has changed since the mid nineteenth century.

Lendenfeld's (1886) comment regarding the fallen snow gums on the Eskdale Spur indicates the residual effects of a bushfire. Strom and Thompson (1936) also reported that a large percentage of snow gums in the Mt Hotham area had been damaged by fire, and Costin (1957) recorded that many of the snow gum islands on the Bogong High Plains had been extensively modified by fire. When snow gums are burnt they will develop multiple stems from their lignotubers. Ashton & Hargreaves (1983) stated that coppicing may be prolific initially but that the number of shoots diminishes to four or five within 20 years and to two or three within 40 years. Thus, when Lendenfeld (1886: 132) reported 'the scrub became very dense, and to the stunted eucalypti [snow gums] a dense undergrowth of subalpine shrubs was added' he was probably travelling through a stand of snow gums that had been recently burnt. Lendenfeld's (1886) reference to the prolific growth of shrubs supports the work of Williams & Ashton (1987a) who found that shrub seedlings are the first to re-establish in an area burnt by fire.

Those parts of the Bogong High Plains that have not been burnt since European settlement carry snow gums with large boles and smaller trees that appear to be encroaching into the adjacent grasslands (Ashton & Williams 1989). Costin (1957: 19) regarded the original woodlands as consisting of 'fairly open stands of snow gum underlain by a grassy sward with relatively few shrubs'. The increased frequency of fire within the snow gum woodland communities since the 1850s has reduced the age of most stands, caused the stands to take on a scrubby appearance, and promoted the growth of shrubs under and near the snow gum woodlands.

Heathland communities

Heath vegetation occurs naturally on exposed, rocky, relatively snow-free sites adjoining sub-alpine woodland and alpine herbfield (Costin 1957). Mueller referred to the presence of shrubs below the summits of Mounts Feathertop and Loeh in 1854, and Lendenfeld (1886) described their association with the snow gum woodlands on the northern face of Mt Bogong in 1886, but few other 19th Century visitors mentioned them. Most writers preferred to describe the snow gum, grassland and/

or the mossland communities of the Bogong High Plains area (Neumayer 1869; Howitt 1877; Stirling 1886; *Illustrated Australian News* 1888; Stirling 1890; Walter 1889).

However, by the early 20th Century a number of authors began to refer to shrublands. In 1900, Maiden (1900: 47) recorded that 'the predominant vegetation [at Mt Hotham], all of which is dwarf, appeared to be *Kunzea muelleri* [Yellow Kunzea], but there were also *Grevillea australis* [Alpine Grevillea] and *Epacris microphylla* [Coral Heath]', all of which are shrubs. Two points are noteworthy here. Firstly, when Stirling visited Mt Hotham in 1887 his description of the summit area featured grasses and herbs and very little reference was made to shrubs (Stirling 1887). Secondly, Maiden (1900) indicated that the shrubs were small. These two comments, in association with the previous descriptions of Mt Hotham, suggest that there was a change in the dominant vegetation of the area from grassland to shrubland just before the turn of the century. In 1910, the vegetation cover of the Bogong High Plains was described by Callanan (1910) as consisting of grasses and herbs and 'besides these there is a prolific growth of heath, varying in height from a few inches on the ridges to a couple of feet on the sidelings'. Callanan wrote as if the growth of heath was a recent phenomenon.

The historic records of heathland vegetation cover suggest that there was a trend towards increasing shrub cover on Mt Hotham and the Bogong High Plains around the turn of the century. Costin reported that heaths had 'invaded large areas of woodland, grassland and herbfield' in the Bogong High Plains area following the 1939 fires. Carr (1962, 1977) suggested that many shrubs show regeneration patterns and at senescence may be replaced by grassland communities. Williams & Ashton (1988) demonstrated, in one of the vegetation plots in Rocky Valley which had remained ungrazed since the mid 1940s, that the shrubs dating from the 1939 fires had begun to die back by the late 1980s and that the gaps established by the senescent shrubs were being colonised by grassland species. Williams & Ashton (1988) further proposed that the transition from grassland to heathland and back to grassland again was a cyclical pattern of at least 30 to 50 years, which was initiated by disturbance due to fire and/or grazing. The historic evidence suggests that, although shrubs have always been a component of the subalpine vegetation, the relative cover of shrubs increased around the turn of the century, peaked following the 1939 fires, and has remained static since then.

Grassland communities

The most distinctive plant communities of the subalpine area of the Bogong High Plains area have always been the grasslands. In 1854, Mueller described the summits of Mounts Loch and Feathertop as 'being covered with alpine herbs and grasses' (Mueller 1855). In 1878, Murray (1878) reported the Bogong High Plains were 'open undulating plains and moors', and in 1886 the summit of Mt Bogong was referred to as an 'alpine meadow' by Lendenfeld (1886), and as 'grassy depressions' carrying 'splendid pasturages' by Stirling (1886). In 1926, the Bogong High Plains were recorded by Tadgell (1926) as being 'generally grassy'. In 1928, the Redbank Plain area at the head of the Victoria River was reported to be a well-grassed valley (Williamson 1929), and in 1936, Guy (1936) described the Bogong High Plains as consisting of 'wide open valleys with luxurious grass'. A detailed sketch of the Bogong High Plains made in 1888 confirms the idea that grasslands dominated the vegetation of the subalpine areas and that they formed an almost continuous cover over the plains. Although the grasslands have always been a distinct feature of the treeless sector of the Bogong High Plains area, it is evident that the geographic extent of grassland cover has declined as shrublands have expanded. The relative cover of grassland has declined because the shrubs typically colonise grassed areas.

Those areas of grasslands not invaded by shrublands have been subject to another noteworthy trend. Since European use of the area commenced, there has been erosion in the grasslands and herbfields. This is evidenced by the following progression of comments. In 1878, Murray (1878) described the Bogong High Plains as 'stony but well grassed'. Eight years later, Lendenfeld (1886) recorded that the summit of Mt Bogong was an 'alpine meadow, studded here and there with protruding rocks'. The Mt Hotham area was described in 1890 by Stirling (1890) as being 'undulating stony ridges alternating with grassy valleys', and in 1899 by Walter (1899) as 'grassy slopes [which] appeared in many places like a carpet'. These quotations indicate that the grassland of the plateaux parts of the Bogong High Plains area were not continuous but were interrupted by bedrock outcrops at intervals.

However, around the turn of the century, the descriptions of the grasslands began to change. For example, in 1904, Coghill (1904: 157) wrote: 'the plateau around the cairn [of Mt Bogong] shows no compact mass of vegetation. Bunches of grass alternate with large patches of barren ground'. In

1910, Callanan (1910) reported that 'the entire area [of the Bogong High Plains] is stony with rocky outcrops forming prominent features throughout'. In 1922, Tadgell (1922: 108) reported that 'there are numerous barren and coarse stony places [on Mt Hotham] where the surface soil has been washed away into the valley'. In the 1930s, Strom & Thompson (1936: 12) recorded that 'the undergrowth on some hill slopes [around Mt Hotham] was practically missing, the surface being covered with rock fragments'. Photographic evidence from the 1930s attests to the extent of bare ground on the Mt Hotham summit. Later, Costin (1957: 19, 21) reported that by the 1950s 'incipient erosion' of the grasslands was widespread and that 'accelerated erosion involving the loss of large quantities of soil has occurred on Mt Bogong'.

The decline in grassland cover and the increase in bare ground can be dated from the turn of the century. Erosion in the grassland areas appears to have peaked by the 1930s, and has steadily declined since the introduction of grazing controls in the 1940s. For those areas where grazing was continued, Carr & Turner (1959) reported that there was an increase in the cover of snowgrass (*Poa* spp.) and a decline in the herb component between 1947 and 1958. Thus, many grassland communities in the subalpine parts of the Bogong High Plains area have either been invaded by shrubs or have seen a change in the composition and cover of the plants present, depending on their location and availability for grazing.

Extensive erosion

Eroded areas in the subalpine parts of the Bogong High Plains area were often noted by visitors during the early 20th Century. Erosion in the grasslands was especially conspicuous, but they were not the only areas affected. Strom & Thompson (1936) mentioned that erosion had occurred in the snow gum woodlands at Mt Hotham, and Costin (1957) reported that the deterioration of mossbeds had occurred in many places in the Bogong High Plains area. The degree of erosion became so pronounced during the early to mid 20th Century that 'erosion pavements' began to form on the plateaux areas. On the steeper slopes, such as along the Razorback south of Mt Feathertop, Costin (1957: 19) claimed that 'deterioration has advanced to the scree stage'. These observations are supported by photographic evidence of the Mt Bogong area.

Lee (1978) claimed that erosion pavements were initiated in grasslands when the degree of vegetation cover declined and the soil between the

thinning tussocks was blown away. This resulted in a lowering of the soil surface. Stones that were naturally present in the soil profile became concentrated as erosion continued, and resulted in the formation of a pavement of stones that formed the new lower surface level. Then, depending on the amount of soil still remaining below the erosion pavement, shrubland or grassland species colonised the eroded area. Lee (1978) stated that:

Where some topsoil still remains, shrubs will dominate—possibly permanently, depending on the conditions. But if little topsoil has yet moved, snow grass tussocks interspersed with the larger herbs like the well-known billy buttons will, in time, come to dominate once more. In alpine and subalpine Australia the vegetation always moves, if not disturbed, towards a climax ground cover of perennial grasses and other herbs, provided enough topsoil remains to permit it.

This is indeed what has happened in the alpine and subalpine parts of the Bogong High Plains area since the 1940s: the eroded areas dominant in the 1920s and 1930s were mostly colonised by shrublands. Without disturbing agents such as fire and excessive grazing, shrublands have begun to revert to grasslands today (Williams & Ashton 1988).

Mosslands

The final vegetation communities of the Bogong High Plains area that have captured the interest of visitors to the area are the mosslands. In 1888, a visitor to the Bogong High Plains reported that (*Illustrated Australian News* 1888: 2):

Here and there are bright yellow spots, which by their smoothness and softness invite you to rest on them. But beware! They are snow moss, and would inevitably swallow you up, horse and all ...

In 1890, Stirling (1890: 45) referred to 'the vivid green of the moss banks' in the Mt Hotham area. The yellow mosslands were probably *Sphagnum* dominated, whereas the green mosslands may have been cushion plants (*Scleranthus biflorus*). In 1910, Callanan (1910) recorded that 'a large area [of the Bogong High Plains] is swampy, covered with heath and moss, with soil of a boggy, peaty nature'. In 1923, Williamson (1923: 91) described the mossland communities as follows:

Proceeding a mile or two further, we came to 'Pretty Valley'—a broad plain traversed by winding streams, the banks of which, in places, almost hid the water ... One had to be careful, or, rather, to allow one's mount to exercise care, in crossing the small streams, whose banks consisted of moss and other matted vegetation.

It is noteworthy that the 1888 writer claimed that a horse would sink out of sight into a moss-bed, whereas in 1923 Williamson recorded that the mossbeds could be crossed on horseback, albeit if a great amount of care was taken. Other visitors of the 1920s and 1930s commented on the 'two fine *Sphagnum* mossbeds' near Maddisons Hut on Mt Bogong (Tadgell 1926: 64), the 'huge moss-bed' in Pretty Valley (Tadgell 1926: 23), a 'large mossy spring' at Redbank Plain on the Victoria River (Williamson 1929: 271), and 'extensive moss beds' in the Rocky Valley and Pretty Valley areas of the Bogong High Plains (Guy 1935: 7). The distinct floral composition and high moisture content of the mossbeds captured the attention of early visitors to the Bogong High Plains area.

However, as with the other plant communities of the area, the mosslands have undergone a change since European use of the area began. This is best illustrated by reference to several individual mossbeds. A 1907 photograph of the Mt Feathertop area featured a small pool typical of *Sphagnum* mossbed communities. However, by the 1950s 'the last accessible bog of any size near Mt Feathertop ... [had] almost disappeared' (Costin 1957: 29) and today does not exist. The previous existence of good mossland specimens on Mt Hotham is evidenced by Stirling's (1890) reference to the 'vivid green of the moss banks'. Mt Loch also supported these communities, but Edmonson (1984: 97) recorded that due to mining traffic over the mountain in the 1880s, 'one moss bed on Mt Loch was practically obliterated'. In the mid 1950s, Costin (1957: 29) reported that 'deterioration has proceeded so far on Hotham and Loch that they are now virtually "dry" mountains'. The 'moss and matted vegetation' present in Pretty Valley on the Bogong High Plains in 1923 (Williamson 1923) were burnt in 1926 as Edmonson (1984: 46) described:

The hasalt plain north of Mt Flora [Mt Jim] which was of a peaty nature was badly affected [by the 1926 fires] and smouldered indefinitely. A very heavy deluge of rain eventually fell on the dry ashes, and when this occurs, the whole surface comes off.

Apparently that mossbed never recovered as it was later mapped as a 'relic bog' (Victorian Conservation Trust & Soil Conservation Authority 1982). Other parts of the Bogong High Plains have also undergone severe modification. Costin et al. (1959: 20) stated that:

Snow pole lines on the Bogong High Plains, in terms of existing conditions make long and unnecessary detours to the heads of the valleys to avoid bogs which are now no more. At the time

when these snow poles were put in it can be assumed that the valleys which can now be crossed so easily were too wet and boggy to be safe.

Costin (1957) also reported that by the 1950s advanced erosion had occurred in mossbeds in Rocky Valley, near Ruined Castle, and at the head of the Big River west of Mt Nelse. On Mt Bogong, the only mossbeds still in existence in 1924 were located on the eastern slope, and included 'two fine *Sphagnum* moss beds' (Tadgell 1924). Others used to exist, but by the 1950s 'the only large bog in the summit area of Mt Bogong—at Stirlings Gap—has been seriously damaged and is rapidly eroding' (Costin 1957: 25). These examples suggest that the cover of mosslands in the Bogong High Plains area in the 1950s is a shadow of that which was originally present.

It appears that until the mid to late 19th Century both the extent and depth of the mossland communities in the Bogong High Plains area far exceeded that of the 20th Century. Ashton & Williams (1989) considered that a climax mossland community was typified by prominent hummocks of *Sphagnum* interspersed with *Carex* dominated ponds, all of which have a high water holding capacity and a high surface roughness. They stated that water movement within an undisturbed mossbed is retarded and, although some channelled flow occurs, the water tends to move on a wide front through the system rather than over its surface. This general description is again supported by both early photographs and writings. However, the mossbeds did not remain in their original condition due to the following factors (Wimbush & Costin 1983: 152):

As a consequence of burning and grazing, surface roughness is reduced and the velocity of the runoff water is increased. Livestock tracking and trampling also have the effect of joining up naturally discrete *Carex* hollows. Incision and erosion of the soft underlying peat follow. A gully may then develop along the valley. As vertical and lateral incision increases, more of the high runoffs are contained as erosive, near-bank-full discharges from the catchment instead of spreading across the valley floor as a whole.

Van Rees (1984) found that cattle do not find mossland species palatable, but that they used the communities extensively because they were the primary source of water on the High Plains. Trampling of the mossbeds by stock led to channellisation and erosion of the stream banks, which became most obvious in Pretty Valley. This process appears to have been well advanced by the 1920s. Tadgell's (1926: 37) observation that the 'water courses of the now dried up springs

had cut deeply into the mountain sides' and photographic evidence from the 1920s both indicate severe erosion of the mosslands.

Since the 1920s, there has been some improvement in the areal extent of mossland vegetation. Carr (1977) reported that a mossbed that had been fenced off from grazing had increased in size and wetness since 1945. McDougall (1989) demonstrated that the same mossbed contained a large unbroken layer of *Sphagnum* moss that trapped most of the water flowing through it. Thus, it appears that the vertical and lateral extent of the mossbeds of the Bogong High Plains area diminished substantially late last century and early this century to a minimum level in the 1920s, but that there has been a small increase in mossbed cover since the 1930s, especially in the ungrazed areas.

A TEMPORAL MODEL FOR VEGETATION CHANGE

Now that the land use, fire and vegetation history of the Bogong High Plains have been discussed, it is appropriate to present a chronological synthesis of those vegetation changes. Fig. 6 has been compiled to assist in this task, and presents sequential information on grazing, fire and intensive land uses. The regularity of visitation to the area between the 1850s and 1950s is noteworthy. The three decades of the 1880s, 1920s and 1940s were particularly well represented for written records of the Bogong High Plains area. Along with known trends in land use and fire history, Fig. 6 also denotes trends in the four vegetation communities based on the evidence presented in the previous section.

It is evident from Fig. 6 that the four main land uses have affected the area during different time periods. The major phase of mining activity was during the 1860s, 1870s and 1880s, and particularly during the 1880s. Grazing by introduced stock occurred between the 1860s and the present with most activity occurring during the six decades between the 1880s and 1940s. The two summers of 1901–02 and 1914–15 saw excessive numbers of stock grazed on the Bogong High Plains and adjacent peaks. Hydroelectric development did not commence until the late 1930s and intensive tourism until the late 1940s. Each land use has played a role in vegetation alteration: particularly mining in the initiation of a modified fire regime, and grazing in extensive vegetation change.

The fire history of the Bogong High Plains area has resulted in noticeable changes in two of the four vegetation communities under consideration.

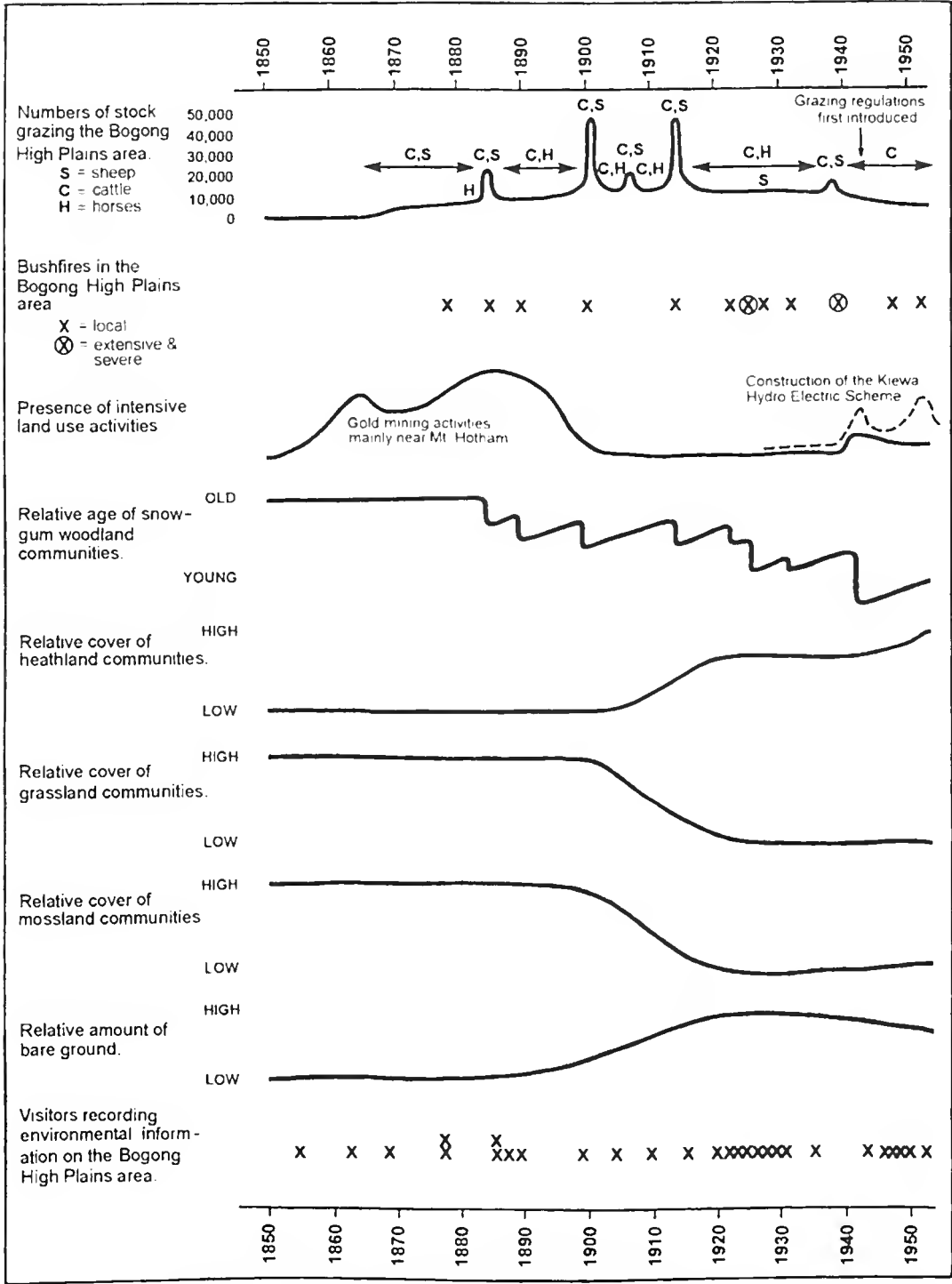


Fig. 6. A temporal model depicting visitor records, land use, fire and vegetation trends in the Bogong High Plains from the 1850s to 1950s.

The distribution of snow gum woodlands has remained largely unchanged but their age has generally decreased due to fire. The increasing incidence and severity of fire between the 1880s and 1939 resulted in a reduction of the age of most snow gum stands. Likewise, the increasing cover of shrublands that occurred after the turn of the century can be partially attributed to the increasing incidence and severity of fire. This modified fire regime occurred in response to fires deliberately lit by miners and graziers in combination with a decline in precipitation between the 1880s and 1940s (Lawrence 1998a).

As mining activities waned and grazing activities intensified after the 1880s, other changes in vegetation characteristics occurred. It seems that the transition from a grass-dominant to shrub-dominant landscape coincided with the years of excessive grazing activities around the turn of the century. One result of overgrazing during the drought years early this century was the decline in grasses and forbs that were palatable to stock. Disturbance of the grassland communities by stock compounded those areas already disturbed by fire and produced additional areas suitable for shrub colonisation. Erosion pavements began to form at about the same time. Excessive grazing activities early this century contributed to an increase in the relative cover of shrubland, a decrease in the proportion of grassland cover, and an increase in the relative amount of bare ground on the Bogong High Plains and surrounding peaks (Fig. 6). It seems that mossbed deterioration and the decline in the perpetuity of the alpine streams also occurred at this time. There is an indication that the summits of Mounts Hotham, Feathertop and Bogong began to demonstrate vegetation change and erosion up to two decades before the Bogong High Plains. The concentration of higher grazing activities on these summits during the 1900s and 1910s is the reason for this.

Contemporary writers were also specific in the reasons for vegetation change in the area. Early authors attributed changes in vegetation primarily to cattle grazing activities (Maiden 1900). Visitors of the 1930s were not so specific and claimed the combined factors of fire, mining and grazing activities had produced the vegetation changes. In the 1950s, the causal factors were deemed to be grazing, fire and engineering works (Costin 1957). Indeed, the temporal model presented in Fig. 6 affirms the opinions of contemporary authors that a combination of grazing activities, fire and intensive land use activities produced vegetation change and deterioration.

It was not until the 1940s that any management

strategies were introduced to redress the decline in vegetation cover and diversity. The management of the Victorian high country originated from concern for the possible siltation of reservoirs in lowland areas. During the 1930s, representatives of the State Rivers & Water Supply Commission visited the Bogong High Plains area and related the damaging influence of fire, mining and grazing activities in the area to siltation of the Hume Reservoir. The formation of the Soil Conservation Board, research into the effects of grazing on the Bogong High Plains environment, and the establishment of an 'Advisory Committee' soon followed. The role of the Advisory Committee was to regulate the numbers, type, and dates of entry and departure of stock to the Bogong High Plains area. A Royal Commission into the grazing of Victorian forest lands (Stretton 1946) resulted in the establishment of the Land Utilisation Council in 1950. The Council prohibited firing by graziers throughout the high country, banned sheep in the high country, and prohibited grazing on the summit of Mt Bogong in 1955 and in the Mounts Feathertop, Hotham and Loeh areas in 1958 (Mosley 1988). Thus, management decisions to protect the alpine and subalpine areas of the Bogong High Plains area were instituted some 50 to 60 years after a deterioration in the environment of the area was first noted.

Today, the environment of the Bogong High Plains area remains dynamic with the vegetation cover of the area still in transition between a degraded and a climax condition (Williams & Ashton 1987b; Wahren et al. 1994).

REFERENCES

- APLIN, G., MITCHELL, P., CLEUGH, H., PITMAN, A. & RICH, D., 1995. *Global Environmental Crises: An Australian Perspective*. Oxford University Press, Melbourne, 317 pp.
- ANDREWS, A. E. J., ed., 1981. *Hume and Hovell, 1824*. Blubber Head Press, Hobart.
- ASHTON, D. H. & HARGREAVES, G. R., 1983. Dynamics of subalpine vegetation at Echo Flat, Lake Mountain, Victoria. *Proceedings of the Ecological Society of Australia* 12: 35–60.
- ASHTON, D. H. & WILLIAMS, R. J., 1989. Dynamics of subalpine vegetation in the Victorian region. In *The scientific significance of the Australian Alps*, R. Good, ed., *Proceedings of the First Fenner Conference on the Environment*, Canberra, September 1988. Australian Alps National Parks Liaison Committee & Australian Academy of Science, Canberra, pp. 143–168.

- AUSTRALIAN ACADEMY OF SCIENCE, 1957. *Report on the conditions of high mountain catchments of New South Wales and Victoria*. Australian Academy of Science, Canberra, 62 pp.
- BELL, M. & WALKER, M. J. C., 1992. *Late Quaternary Environmental Change: Physical and Human Perspectives*. Longman Scientific & Technical, New York, 273 pp.
- BEST, D., 1920. To the Alps for Coleoptera. *Victorian Naturalist* 37: 85–90.
- BOLTON, G., 1992. *Spoils and spoilers: a history of Australians shaping their environment*, 2nd edn. Allen & Unwin, Sydney, 190 pp.
- CABENA, P. B., 1980. *Grazing the high country: an historical and political geography of high country grazing in Victoria, 1835 to 1935*. Unpublished Master of Arts Thesis, Department of Geography, University of Melbourne, 182 pp.
- CALLANAN, S. 1910. Unpublished report from Mr S. Callanan, Assistant Surveyor, to Mr J. M. Reed, Surveyor General, 8-4-1910, entitled 'Re: Bogong High Plains'. File No. T74607. Department of Crown Lands and Survey, Melbourne, 3 pp.
- CARR, S. G. M., 1962. The discovery of the Bogong High Plains. *Proceedings of the Royal Society of Victoria* 75: 285–289.
- CARR, S. G. M., 1977. *Report on inspection of the Bogong High Plains: 1977*. Unpublished report. Research School of Biological Sciences, Australian National University, Canberra, 22 pp.
- CARR, S. G. M. & TURNER, J. S., 1959. The ecology of the Bogong High Plains. I. The environmental factors and the grassland communities. *Australian Journal of Botany* 7: 12–33.
- COGHILL, G., 1904. The Buffalo mountains camp-out: Thursday 24th December, 1903 to Monday 4th January, 1904. *Victorian Naturalist* 20: 144–159.
- COMMINS, J., 1995. New South Wales bushfires. *Voice of the Mountains* 18: 32.
- COMMONWEALTH OF AUSTRALIA, 1996. *Australia: State of the Environment 1996*. CSIRO, Melbourne.
- COSTIN, A. B., 1957. *High mountain catchments in Victoria in relation to land use*. Soil Conservation Authority, Melbourne, 83 pp.
- COSTIN, A. B., WIMBUSH, D. J., KERR, D. & GAY, L. W., 1959. Studies in catchment hydrology in the Australian Alps. I. Trends in soil and vegetation. *CSIRO Division of Plant Industry Technical Paper* No. 13, 36 pp.
- DEACON, E. L., 1953. Climatic change in Australia since 1880. *Australian Journal of Physics* 6: 209–218.
- DODSON, J., ed., 1992. *The Naive Lands: Prehistory and Environmental Change in Australia and the Southwest Pacific*. Longman Cheshire, Melbourne, 258 pp.
- DOVERS, S., ed., 1994. *Australian Environmental History: Essays and Cases*. Oxford University Press, Melbourne, 281 pp.
- EDGEHILL, M. C. R., 1973. *Nature and perception of the bushfire hazard in southeastern Australia*. Monash Publications in Geography No. 5. Department of Geography, Monash University, Melbourne, 51 pp.
- EDMONDSON, J. W., 1984. Bogong High Plains. *Voice of the Mountains* 8: 46–50.
- FAWCETT, S. G. M., 1955. *Upper Hume catchment: ecological report*. Unpublished report. Soil Conservation Authority, Melbourne, 127 pp.
- FINN, E., 1888. *The chronicles of early Melbourne 1835 to 1852: historical, anecdotal and personal*, by 'Garryowen'. Fergusson & Mitchell, Melbourne.
- FLOOD, J., 1980. *The moth hunters: Aboriginal prehistory of the Australian Alps*. Australian Institute of Aboriginal Studies, Canberra, 388 pp.
- FOLEY, J. C., 1947. A study of meteorological conditions associated with bush and grass fires and fire protection strategy in Australia. *Commonwealth Bureau of Meteorology Bulletin* No. 38.
- GOOD, R. B., 1992. Fire Management in the Australian Alps. *Revue de Géographie Alpine* 2–3: 451–477.
- GOUDIE, A., 1992. *Environmental Change: Contemporary Problems in Geography*, 3rd edn. Oxford University Press, Oxford, 329 pp.
- GOUDIE, A. & VILES, H., 1997. *The Earth Transformed: An Introduction to Human Impacts on the Environment*. Blackwell Publishers, Oxford, 276 pp.
- GUY, L. T., 1935. *Hydroelectric schemes: report by civil engineer*. Unpublished report. State Electricity Commission, Melbourne.
- GUY, L. T., 1936. Snow studies on Bogong High Plains by State Electricity Commission of Victoria, Australia. In *Kiewa Scheme: Folder No. 3: Hydrological data*. Unpublished report. State Electricity Commission, Melbourne, 48 pp.
- HARDY, W. A., 1956. *Middle Creek-Bundarra River assessment: 1955–56*. Forests Section, Internal Report No. 55/1490. Department of Conservation, Forests & Lands, Swifts Creek.
- HOLTH, T., 1980. *Cattlemen of the high country*. Rigby, Adelaide, 152 pp.
- HOLTH, T. & HOLTH, J., 1985. *Challenge of the high country*. Rigby, Adelaide, 152 pp.
- HOWITT, A. W., 1877. Notes on the geological structure of North Gippsland. *Geological Survey of Victoria Progress Report* 4: 75–117.
- HOWITT, A. W., 1879. Report of the Crown Lands Commission of Inquiry on both the agricultural and pastoral occupation of the public lands to be instituted on the expiration of the present Land Act at the close of 1880. Evidence presented by A. W. Howitt 22-1-1879 at Bairnsdale. *Victorian Parliamentary Paper* No. 73, pp. 328–331.
- ILLUSTRATED AUSTRALIAN NEWS, 22-12-1888. Article entitled 'The Bogong High Plains', p. 2.
- JOHNSON, D., 1974. *The alps at the crossroads*. Victorian National Parks Association, Melbourne, 208 pp.
- KERSHAW, A. P. & STRICKLAND, K. M., 1989. The development of alpine vegetation on the Australian mainland. In *The scientific significance of the Australian Alps*, R. Good, ed. Proceedings of the First Fenner Conference on the Environment, Canberra, September 1988. Australian Alps National Parks Liaison Committee & Australian Academy of Science, Canberra, pp. 113–126.

- KIRKPATRICK, J., 1994. *A continent transformed: human impact on the natural vegetation of Australia*. Oxford University Press, Melbourne, 133 pp.
- KIRKPATRICK, J. B. & DICKINSON, K. J. M., 1984. The impact of fire on Tasmanian alpine vegetation and soil. *Australian Journal of Botany* 32: 613–629.
- KOHEN, J. L., 1995. *Aboriginal environmental impacts*. University of New South Wales Press, Sydney, 160 pp.
- LAWRENCE, R. E., 1994. Environmental changes on the Bogong High Plains, 1850s to 1990s. In *Australian Environmental History: Essays and Cases*, S. Dovers, ed. Oxford University Press, Melbourne, pp. 167–197.
- LAWRENCE, R. E., 1995. The effects of grazing activity on the hydrology of the Bogong High Plains, Australia. *The Rangeland Journal* 17: 138–153.
- LAWRENCE, R. E., 1998a. Historical ramifications of climate change in the Alpine National Park. In *Celebrating the parks: a symposium on parks history: proceedings*, E. Hamilton-Smith, ed. Mt Buffalo Chalet, Victoria, 16–19 April 1998.
- LAWRENCE, R. E., 1999. The impact of land cover changes on hydrological sustainability in the Victoria alpine area. *Proceedings of the Royal Society of Victoria* 111: iii–iii.
- LEE, B., 1979. A high-country perspective. *Ecos* 22: 24–31.
- LEIGH, J. H., WIMBUSH, D. J., WOOD, D. H., HOLGATE, M. D., SEE, A. V., STANGER, A. G. & FORRESTER, R. I., 1987. Effects of rabbit grazing and fire on a subalpine environment. 1. Herbaceous and shrubby vegetation. *Australian Journal of Botany* 35: 433–464.
- LENDENFELD, R. V., 1886. An exploration of the Australian Alps. *Transactions of the Geological Society of Australasia* 1: 119–133.
- MACKENZIE, F. T. & MACKENZIE, J. A., 1995. *Our Changing Planet: An Introduction to Earth System Science and Global Environmental Change*. Prentice Hall, New Jersey, 387 pp.
- MCDUGALL, K., 1982. *The alpine vegetation of the Bogong High Plains*. Ministry for Conservation Environmental Studies Publication No. 357. Ministry for Conservation, Melbourne, 126 pp.
- MCDUGALL, K., 1989. *The Effect of Excluding Cattle from a Mossbed on the Bogong High Plains, Victoria*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 95, 19 pp.
- MAIDEN, J. H. 1900. Some notes of a trip to the Victorian Alps. *Victorian Naturalist* 17: 43–47.
- MANNION, A. M., 1991. *Global Environmental Change*. Longman Scientific & Technical, New York, 404 pp.
- MITCHELL, A., 1968. Range management, catchments and conservation. *Victoria's Resources* 10: 15–18.
- MOSLEY, G., 1988. *Australian alps world heritage nomination proposal*. Victorian National Parks Association, Melbourne, 124 pp.
- MUELLER, F. 1855. *Annual report of the Government Botanist*. Government Printer, Melbourne, 2 pp.
- MURRAY, R. A. F., 1878. Report on the geological survey of portions of Dargo and Bogong. *Geological Survey of Victoria Progress Report* 3: 96–117.
- NEUMAYER, G., 1869. *Results of the magnetic survey of the Colony of Victoria*. J. Schneider, Mannheim, 197 pp.
- NOBLE, W. S., 1977. *Ordeal by fire: the week a state burned up*. Hawthorn Press, Melbourne, 85 pp.
- OLLIER, C. D. & WYBORN, D., 1989. Geology of alpine Australia. In *The scientific significance of the Australian Alps*, R. Good, ed. Proceedings of the First Fenner Conference on the Environment, Canberra, September 1988. Australian Alps National Parks Liaison Committee & Australian Academy of Science, Canberra, pp. 35–53.
- PATTON, R. T., 1953. Ecology of the Bogong High Plains. *Victorian Naturalist* 69: 137–142.
- PEARSON, A. M., 1969. *Echoes from the mountains and history of the Omeo Shire Council*. Omeo Shire Council, Omeo, 404 pp.
- PITTOCK, A. B., 1975. Climatic change and patterns of variation in Australian rainfall. *Search* 6: 498–504.
- ROBERTS, N., 1989. *The Holocene: An Environmental History*. Blackwell Publishers, Oxford.
- ROBERTS, N., ed., 1994. *The Changing Global Environment*. Blackwell Publishers, Oxford, 531 pp.
- RUSII, B. J., 1939. The bush fires at St Bernard. *Schuss* 5: 60–63.
- SCHUSS, 1939. Article entitled 'Bush fire damage in the Alps' in vol. 5: 66–68.
- SIMMONS, I. G., 1989. *Environmental History: A Concise Introduction*. Blackwell Publishers, Oxford, 206 pp.
- SIMMONS, I. G., 1993. *Changing the Face of the Earth: Culture, Environment, History*. Blackwell Publishers, Oxford, 487 pp.
- SLATTERY, D., 1998. *The Australian alps: Kosciuszka, Alpine and Namadgi National Parks*. University of New South Wales Press, Sydney, 233 pp.
- SLATYER, R. O., 1989. Alpine and valley bottom tree-lines. In *The scientific significance of the Australian Alps*, R. Good, ed. Proceedings of the First Fenner Conference on the Environment, Canberra, September 1988. Australian Alps National Parks Liaison Committee & Australian Academy of Science, Canberra, pp. 169–184.
- SMART, B. K., 1883. Beechworth mining district: Buckland division. In *Reports of the mining surveyors and registrars: quarter ending 30th September 1883*. Mines Department, Melbourne, p. 32.
- STEPHENSON, H. H., ed., 1980. *Cattlemen and huts of the High Plains*. Graphic Books, Melbourne, 350 pp.
- STRETTON, L. E. B., 1939. *Report of the Royal Commission to inquire into the causes of and measures taken to prevent the bushfires of January, 1939, and to protect life and property and the measures to be taken to prevent bushfires in Victoria and to protect life and property in the event of future bushfires*. Parliamentary Paper 6912/39. Government Printer, Melbourne.

- STRETTON, L. E. B., 1946. *Report of the Royal Commission to inquire into forest grazing*. Parliamentary Paper 1945/47. Government Printer, Melbourne.
- STIRLING, J., 1886. Notes on Mount Bogong. *Transactions of the Geological Society of Australasia* 1: 134-136.
- STIRLING, J., 1887. Notes on the flora of Mount Hotham. *Victorian Naturalist* 4: 72-78.
- STIRLING, J., 1890. Physiography of Mount Hotham and surroundings. *Transactions of the Royal Society of Australasia* 8: 43-57.
- STROM, H. G. & THOMPSON, G. T., 1936. *Report on inspection of the Hume Reservoir catchment*. Internal report. State Rivers & Water Supply Commission, Melbourne, 19 pp.
- TADGELL, A. J., 1922. A contribution to 'the flora of the Victorian Alps'. *Victorian Naturalist* 38: 105-118.
- TADGELL, A. J., 1924. Mount Bogong and its flora. *Victorian Naturalist* 41: 56-80.
- TADGELL, A. J., 1926. Mount Faintner and beyond. *Victorian Naturalist* 43: 32-47.
- TADGELL, A. J., 1930. Mount Nelson and its surroundings. *Victorian Naturalist* 46: 227-235.
- THE AGE, 1914. Article entitled: 'State forests: devastation by fires: last summer's record: vast areas swept: amended legislation urgently demanded' in edition 4-5-1914, p. 11.
- TURNER, J. S. & FAWCETT, S. G. M., 1946. *Ecological work on the High Plains, Bogong, in connection with soil erosion: interim report*. Unpublished report. Botany School, University of Melbourne, 20 pp.
- TURNER, H. G., 1904. *A history of the colony of Victoria*. Longmans, Green & Co., London.
- TURNER, J. S. & FAWCETT, S. G. M., 1948. *Ecological work on the High Plains, Bogong, in connection with soil erosion: second report*. Unpublished report. Botany School, University of Melbourne, 37 pp.
- VAN REES, H., 1984. *Behaviour and diet of free-ranging cattle on the Bogong High Plains, Victoria*. Department of Conservation, Forests & Lands Environmental Studies Publication No. 409. Department of Conservation, Forests & Lands, Melbourne, 198 pp.
- VICTORIA, CONSERVATION TRUST & SOIL CONSERVATION AUTHORITY, 1982. *Bogong High Plains: vegetation map and guide to alpine flora: Pretty Valley sheet*. Victoria Conservation Trust & Soil Conservation Authority, Melbourne.
- VICTORIA, DEPARTMENT OF CONSERVATION AND ENVIRONMENT, 1992. *Alpine National Park: Bogong unit: Management plan*. Department of Conservation & Environment, Melbourne, 336 pp.
- VICTORIA, FORESTS COMMISSION, 1983. *Report of the Forests Commission, Victoria, for the year ended 30 June, 1983*. Government Printer, Melbourne.
- VICTORIA, INTERIM REFERENCE AREAS ADVISORY COMMITTEE, 1977. *Estimates of time required for recovery of Victorian plant communities from crown and grass fires*. Land Conservation Council, Melbourne, 26 pp.
- VICTORIA, NATIONAL PARKS SERVICE, 1983. *Bogong National Park: proposed interim management plan*. National Parks Service, Melbourne, 169 pp.
- VICTORIA, SOIL CONSERVATION BOARD, 1945. *Soil Conservation Board, Fifth annual report for the year ended 30th June, 1945*. Government Printer, Melbourne.
- VICTORIA, SOIL CONSERVATION BOARD, 1947. *Soil Conservation Board: Seventh annual report for the year ended 30th June, 1947*. Government Printer, Melbourne.
- VICTORIA, SOIL CONSERVATION BOARD, 1949. *Soil Conservation Board, Ninth annual report for the year ended 30th June, 1949*. Government Printer, Melbourne.
- VICTORIA, STATE ELECTRICITY COMMISSION, 1935. *Kiewa scheme*. Unpublished report. State Electricity Commission, Melbourne.
- VICTORIAN GOVERNMENT, 1926. Forests Act: restrictions on lighting fires etc., in forests. *Victorian Gazette* 26-5-1926, p. 1676.
- WAHREN, C.-H. A., PAPST, W. A. & WILLIAMS, R. J., 1994. Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: an analysis of vegetation records from 1945 to 1994. *Australian Journal of Botany* 42: 607-639.
- WALTER, C., 1899. A trip to the Victorian Alps. *Victorian Naturalist* 16: 81-87.
- WESTON, E. R., 1939. Black-out in the Alps. *Schuss* 5: 70-71.
- WILLIAMS, R. J., 1990. Growth of subalpine shrubs and snow grass following a rare occurrence of frost and drought in southeastern Australia. *Arctic and Alpine Research* 22: 412-422.
- WILLIAMS, R. J. & ASHTON, D. H., 1987a. The composition, structure and distribution of heath and grassland communities in the subalpine tract of the Bogong High Plains, Victoria. *Australian Journal of Ecology* 12: 57-71.
- WILLIAMS, R. J. & ASHTON, D. H., 1987b. Effects of disturbance and grazing by cattle on the dynamics of heathland and grassland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* 35: 413-431.
- WILLIAMS, R. J. & ASHTON, D. H., 1988. Cyclical patterns of regeneration in heathland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* 36: 605-619.
- WILLIAMSON, H. B., 1923. A trip to the Bogong High Plains. *Victorian Naturalist* 25: 88-93.
- WILLIAMSON, H. B., 1929. Plant hunting in the Cobungra district. *Victorian Naturalist* 45: 271-276.
- WIMBUSH, D. J. & COSTIN, A. B., 1983. Trends in drainage characteristics in the subalpine zone at Kosciusko. *Proceedings of the Ecological Society of Australia* 12: 143-154.
- WORSTER, D., ed., 1988. *The Ends of the Earth: Perspectives on Modern Environmental History*. Cambridge University Press, Cambridge.
- YOUNG, A. R. M., 1996. *Environmental Change in Australia Since 1788*. Oxford University Press, Melbourne, 238 pp.

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All manuscripts should be written in clear and concise English. Use double spacing throughout; leave 30 mm margins around the text; number all pages. Underline only those words to be italicised in running text. All measurements are to be expressed in SI units (e.g. μm , mm, m, km, but not cm) and standard symbols used. Authors should follow the layout of headings, tables and illustrations as presented in a recent issue of the *Proceedings*. Papers should be organised as follows:

1. A brief title, capitalised and, if possible, beginning with a key word.
2. The name and address of the author(s), with superscripts to distinguish addresses of multiple authors.
3. A full reference to the paper, leaving space for the printer's additions.
4. A short abstract of not more than 200 words describing the results (rather than the contents) of the paper.
5. The main text. Capitalise the first word of the introductory paragraph; do not use the heading 'Introduction'. Within the text up to three grades of heading may be used, typed as follows:

GRADE ONE HEADING

Grade two heading

Grade three heading. Followed by running text on the same line.

Refer to illustrations of the paper in the text as 'Fig. 1A, B', 'Figs 1, 2' or 'Figs 1-4', and indicate in the margins where the illustrations should be placed. Refer to references in the text as Birch (1985), (Birch 1985) or (Birch 1985: 2, fig. 1); multiple citations of references should be arranged chronologically. All references cited in the text must be listed at the end of the paper. Footnotes in the main text are not allowed.

In taxonomic works, synonymies should be of the same format as the following examples, with a dash preceding authors' names except in the case of reference to the original description.

Eudendrium generalis Lendenberg 1885: 351, pl. 6.—Lendenberg 1887: 16.

Eudendrium generale.—Hartlaub 1905: 515.—Watson 1985: 196-200, figs 40-52.

non *Eudendrium generale*.—Watson 1982: 89, pl. 10, fig. 3.

Eudendrium lendenfeldi Briggs 1922: 150.—Rosler 1978: 104, 120, pl. 20, figs 1-3.

Note that plate and figure numbers, etc. originally given in Roman numerals should be transliterated into Arabic figures; this is also the case in the main text and in the references.

6. *Acknowledgements*. These should follow the main text and be as brief as possible.

7. *References*. These should conform in arrangement to the examples below, but do not type authors' names in capitals. Journal titles must be cited in full as they appear on the title page.

BIRCH, W. D., 1985. Calc-silicate rocks at Toolangi, Victoria. *Proceedings of the Royal Society of Victoria* 97: 1-18.

MACPIERSON, J. H. & GABRIEL, C. J., 1962. *Marine Molluscs of Victoria*. Melbourne University Press, Melbourne, xv+475 pp.

PARSONS, W. T., 1982. Weeds. In *Atlas of Victoria*, J. S. Duncan, ed., Victorian Government Printing Office, Melbourne, 122-125.

8. *Tables and Figures*. Each table with its title should be typed on a separate sheet. A separate sheet should also be used to list captions to figures in numerical order.

ILLUSTRATIONS

These must be designed for one or two column width (67 mm or 140 mm) and should be submitted at reproduction size; maximum length is 193 mm. Photographs should be supplied as unmounted, glossy prints labelled on the back; a Figure that is a composite of several photographs should be mounted on paper (not card). Line drawings should be made in black ink and supplied as glossy or flat prints; scales must be included and compass directions included where necessary. On composite Figures, items should be labelled A, B, C, etc. (not a, b, c). In the case of tables to be reproduced directly from copy, *italic typeface* not underlining must be used for italicised words. Oversize illustrations, tables or maps may be accepted for publication as foldouts only if the author meets all costs involved in their production. Maximum size for foldouts is 193x285 mm.

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